INTERANNUAL VARIABILITY OF EPIBENTHIC COMMUNITIES IN THE CHUKCHI SEA, ALASKA

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31 July 2015
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A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, AK

August 2015

Abstract

Epibenthic communities contain a wide range of organisms and serve an important role in marine ecosystems. They are involved in carbon remineralization, benthic production, and are important prey items for higher trophic levels. Arctic epibenthic communities may be experiencing significant changes in species composition, abundance, and biomass at both short and long term time scales. While epibenthic communities may be responding to long term shifts in the environment, differentiating long term trends from short term interannual variation can be problematic. The present study examined interannual differences of epibenthic communities and potential environmental drivers of their variability in the Chukchi Sea. For this, a plumb-staff beam trawl was used to sample epibenthic species composition, abundance, and biomass of the dominant invertebrate taxa at 71 stations around the Chukchi Sea during the ice free seasons of 2009, 2010, 2012, and 2013. Over the entire study area and within a smaller area with the most temporal coverage, the largest separation was between 2009 and 2013, with more difference between 2009 to 2010 than between 2012 and 2013. Crustaceans were the most significant contributors to community composition, based on abundance, and biomass. The important environmental drivers that varied along with the epibenthic community in some but not all years included bottom water temperature, salinity, dissolved oxygen, mean sediment chlorophyll *a*, and sediment organic matter. In contrast, sediment grain size was important in all years and, therefore, was the least likely to contribute to the biological variability among years. While these data provide a benchmark on interannual variability of epibenthic communities in the Chukchi Sea, more monitoring is essential to determine long term trends.

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Acknowledgements

I would like to thank my advisor Brenda Konar and my committee members, Peter Winsor and Ken Coyle, for their support and guidance during this project. Special thanks to Heather Crowley of the Bureau of Ocean Energy Management for support of COMIDA. Thanks also to Ken Dunton for being the lead PI and to Jackie Grebmeier and Lee Cooper for being Chief Scientists aboard the various cruises. This work could not have been completed without the field assistance of Alexandra Ravelo, Tanja Schollmeier, and Martin Schuster. Thanks to all of the COMIDA PIs and their teams, the Captain and crew of the USCGC Healy, the RV Alpha Helix, the RV Moana Wave, and all supporters of the COMIDA project (BOEM Contract Number UTA11-000873). In addition, special thanks to the Robert Byrd Scholarship Program, the Matthew Iya Memorial Foundation, and the Francis "Bud" Fay Memorial Foundation for additional funding. I would also like to thank Nora Foster, Ben Daly, and Ken Coyle who aided in the identification of many taxa, as well as Bob Clarke, Paul Somerfield, and Katrin Iken who gave their advice and guidance on my statistical analysis. Finally, I would like to thank my family and friends, who provided unconditional support, and without whom this project would not have been possible.

1. Introduction

Similar to other Arctic seas, the Chukchi Sea is a dynamic ecosystem with considerable short term variability in both its biological and physical environment. Short term variability (considered in this study as differences or separation between years) in the abundance and biomass of epibenthic organisms is a natural phenomenon and may be caused by a variety of environmental drivers, including variation in local current regimes, the amount of production that reaches the benthos, and water mass properties (such as temperature and salinity) (Winsor and Chapman, 2002; Blanchard et al., 2013a; Questel et al., 2013). There are three main currents with unique water mass properties that flow northward into the system: Alaska Coastal Water, Anadyr Water, and Bering Shelf Water (Grebmeier, 1987; Grebmeier et al., 1989). Anadyr Water and Bering Shelf water converge to form Bering Shelf-Anadyr Water (Grebmeier et al., 1989). The Alaska Coastal Water flows on the eastern side of the Chukchi Sea, and is characterized by higher temperature and lower salinity than Bering Shelf-Anadyr Water in the west, which is characterized by low temperature and relatively high salinity (Grebmeier et al., 1989). The Alaska Coastal Current can alter direction under particular wind regimes, flowing in a southward direction instead of northward (Weingartner et al., 2005). The Chukchi Sea undergoes large variation in temperature, salinity, and overall flow characteristics of these current regimes on monthly, annual, and even decadal scales (Weingartner et al., 2005). If variation occurs, it can cause a shift in important drivers that shape the structure of benthic communities, including sediment grain size, salinity, temperature, and the quality (carbon and nitrogen content within the sediment) and quantity of production reaching the seafloor (Winsor and Chapman, 2002; Blanchard et al., 2013a; 2013b; Questel et al., 2013). Understanding short term variability is essential if we are to properly interpret long term changes in biological communities.

Previous studies of the Chukchi Sea have found that this region has the highest abundance and biomass of benthic organisms in the Arctic, in spite of the low temperatures and high temporal variation in particulate fluxes to the seafloor (White, 1977; Grebmeier, 1987). Benthic fauna, therefore, play a much greater role in benthic turnover and production in the Arctic than in lower latitudes (Feder et al., 2005; Blanchard et al., 2013a). High benthic abundance and biomass despite the harsh environment have been linked to a high deposition of

organic material, particularly in cold waters (Haflinger, 1981; Stoker, 1981). In addition, benthic community composition is different, and abundance and biomass is higher, in offshore regions compared with the coast in arctic regions (Stoker, 1981). The pattern of abundance, biomass, and overall community composition conforms to current patterns and water mass distributions for the Chukchi Sea as there is a higher macrofaunal abundance and biomass under the offshore Bering Shelf Anadyr Water (1684-6940 ind/ m^2 and 22.2-24.2 g C/m^2, respectively) than under the inshore Alaska Coastal Current (641-4193 ind/m^2 and 2.0-15.4 g C/m^2, respectively) (Grebmeier et al., 1989).

Echinoderms and crustaceans make up the majority of the epibenthic community in the Chukchi Sea, and are, therefore, important in this environment (Piepenburg, 2000; Feder et al., 2005; Bluhm et al., 2009; Ravelo et al., 2014). For example, brittle stars can number as high as several hundred individuals m^2 (Piepenburg, 2000). Both echinoderms and crustaceans play important roles in the remineralization of organic matter, bioturbation of the surrounding sediment, and linking the benthic food chain to higher trophic levels (Piepenburg et al., 1995; Bluhm et al., 1998; Summers and Nybakken, 2000). It has been estimated that a significant portion of energy in Arctic shelf systems may pass through the epibenthos (Piepenburg et al., 1995; Piepenburg and Schmid, 1996). The abundance and biomass of echinoderms and crustaceans are sensitive to the amount of available primary production (McMahon et al., 2006), as well as to the temperature and salinity regimes of various water masses (Grebmeier et al., 1988; Feder et al., 1994). Therefore, echinoderm and crustacean abundance, biomass, and relative community composition can shift along with the seasonal and annual variation in the main currents flowing into the Chukchi, since current variation could cause a shift in the advection of production to the benthic environment. In a previous study, these two taxa varied spatially in both abundance and biomass across the Chukchi Sea, and generally had an inverse relationship in their dominance distribution (Ravelo et al., 2014).

Epibenthic organisms display a variety of sediment regime preferences and are strongly influenced by sediment grain size and quality (carbon and nitrogen content within the sediment) (Taghon, 1982; Etter and Grassle, 1992). For instance, polychaetes and brittle stars dominate in muddy substrates, whereas amphipods and crabs dominate in coarser grained regimes (Highsmith and Coyle, 1992). Finer grained sediments contain more organic matter, and have

higher microbial activity than coarse substrata (Boos and Franke, 2004). Substrate, therefore, strongly influences community composition and likewise provides essential components needed to maintain metabolic processes (Tenore, 1988). If shifts in sediment grain size or sediment quality occur, then changes in benthic communities are expected (Grebmeier et al., 1989). Sediment organic content (hereon referred to as sediment quality) is important in maintaining cellular structure and influences amino acid synthesis (Tenore, 1988). Carbon and nitrogen are therefore needed in a large supply to support the extensive benthic communities. Since sediment grain size and quality are determined by hydrodynamic events such as current speed and duration, sediment quality can be used to infer hydrodynamic processes and physical ocean events, which affect food supply and habitat structure for epibenthic communities. Sediment characteristics are a vital factor in predicting how these communities are structured, both spatially and temporally (Blanchard and Feder, 2014).

In shallow seas, like the Chukchi, particles are quickly advected to the benthos, thus allowing for a fresh supply of productivity to the epibenthic environment. It is ultimately the flux of energy from nutrient rich surface waters to the benthos that links pelagic production to benthic production (Grebmeier and Barry, 1991; Wassmann, 1991; Dunton et al., 2005). Since benthic-pelagic coupling is a product of depth and the amount of pelagic production, which is driven by the advection of nutrient rich waters from the Bering Sea through the Bering Strait into the shallow Chukchi Sea (Coachman et al., 1975; Springer and McRoy, 1993; Grebmeier et al., 2006), tight benthic-pelagic coupling is very important in supporting the large epibenthic communities found in the Chukchi Sea. Organic matter flux to the benthos is highly variable interannually for high latitudes (Wassmann et al., 2006). Overall, abundance and biomass of epibenthic organisms has been decreasing on a decadal time scale in some high latitude regions, and has been thought to be due to a reduction in the amount of carbon flux to the benthos (Baldwin and Smith Jr., 2003). A decrease in benthic-pelagic coupling could put stress on the large epibenthic communities of the Chukchi Sea (Ruhl, 2007), resulting in an overall reduction in organism size (Baldwin and Smith Jr., 2003). Since the Chukchi Sea is such a dynamic environment, benthic community structure may be driven by many environmental drivers. It is, therefore, important to understand which drivers are important in this system, and in particular, which are influencing the short term variability in the biology.

This study presents information on the short term variation of abundance, biomass, and species composition of the epibenthos at stations on the northeastern Chukchi Sea shelf occupied in 2009 – 2013 (Figure 1). Comparisons were made between 2009 and 2010 and between 2012 and 2013 as well as between the earlier and later year groups. The objectives of this current study were to (1) determine the interannual differences in abundance and biomass of epibenthic communities in the Chukchi Sea, (2) determine which species specifically contributed to the interannual differences in community structure, and (3) determine which environmental drivers, if any, influence the community variability. Along with these objectives, the following hypotheses were tested: (1) The epibenthic community structure in the Chukchi Sea will vary interannually, (2) the observed variation in epibenthic community structure is driven by crustaceans and echinoderms, and (3) current regime proxies such as sediment grain size and sediment carbon and nitrogen content will be the main drivers of epibenthic community structure variability.

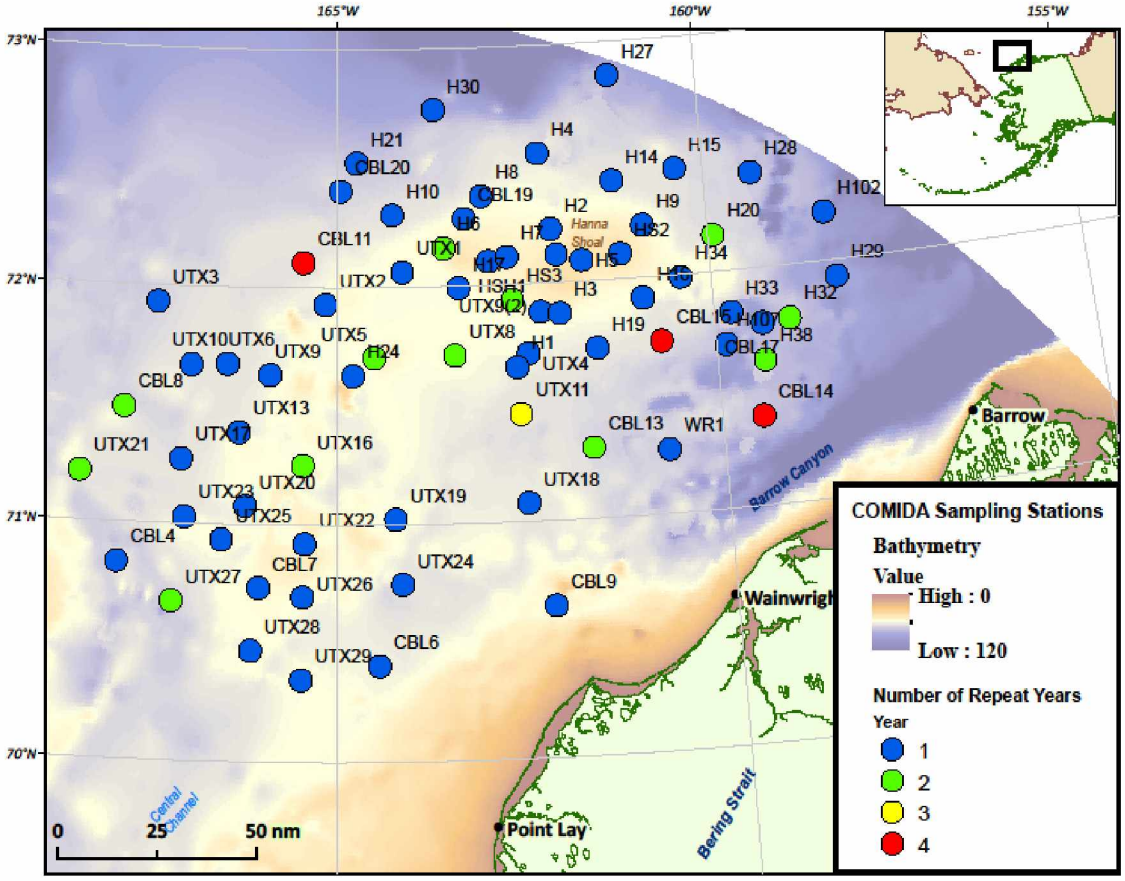


Figure 1: Epibenthic stations sampled in 2009, 2010, 2012, and 2013 in the Chukchi Sea, Alaska. The color of the circles represent the number of years that a station was sampled.

2. Materials and Methods

2.1 Sampling Site Description

The present study was carried out in the northeastern Chukchi Sea, Alaska extending from 70^0 to 73^0N and 168^0 to 157^0W. Sampling took place in the ice-free seasons in 2009 (n=26 stations), 2010 (n=26), 2012 (n=20), and 2013 (n=23). Of the 71 total stations, 24 were sampled in multiple years, with three being sampled all four years (Figure 1). In 2009 and 2010, the study area was more widespread, while the 2012 and 2013 study area focused on the northeast. Stations ranged in depth from 24 to 65 m. In 2009 and 2012, stations were initially selected using a tessellation method in GIS that ensured random selection and even station distribution (White

et al., 1992). The following years (2010 and 2013), stations were again randomly designated; however, some previously sampled stations were opportunistically resampled.

2.2 Sampling Strategy

The epibenthic communities were sampled at each station with a 3.05 m plumb-staff beam trawl (Gunderson and Ellis, 1986). The trawl had a 7 mm mesh and a 4 mm codend liner, and was modified with a lead line and 15 cm chain pieces tied to the footrope every 15 cm to increase connectivity with the seafloor. Bottom time for the trawl ranged from 1 min and 15 sec to 5 min, depending on substrate composition and epifaunal density for each specific area, which was determined visually using a benthic camera deployed prior to each trawl. The resulting trawl sample was then sieved on deck and sorted into the lowest taxonomic level possible, after which taxa were counted and weighed. If a station was resampled, the same trawl parameters were used (wire length, boat speed and bottom time). Data were standardized to 1000 m^2. When a trawl sample was too large to feasibly process, it was subsampled by dividing the sample into equal portions and choosing one portion at random. Any unknown organisms were preserved in a 10% formalin solution for later identification at the University of Alaska Fairbanks.

Environmental drivers were sampled in the same years and at the same stations as the biological data. Sediments were collected with 0.1 m^2 van Veen grabs, and were used for sediment grain size analysis and for determining sediment quality, defined as total organic carbon, total organic nitrogen, sediment chlorophyll *a*, and C:N (details in Grebmeier and Cooper, 1995; Cooper et al., 2002). In addition, water column characteristics (bottom water temperature, salinity, turbidity, dissolved oxygen and pH) were determined via a YSI 6600 V2-4 data sonde (YSI inc, Yellow Springs, Ohio, USA) in 2009 and 2010, and by a Seabird CTD rosette in 2012 and 2013.

2.3 Data Analysis

Data analyses were performed through ArcGIS, PRIMER v. 6 (Clarke and Gorley, 2006), and R (www.r-project.org, V2.15.0). As an initial examination into the study area, a CLUSTER analysis was run on the proportion, or relative, abundance and biomass of major taxa in PRIMER to determine how stations grouped together based on taxon similarity both spatially and temporally. This was done via a similarity matrix utilizing the Bray-Curtis coefficient on 4^{th} root

transformed data. The SIMPROF routine was then used to determine significantly different cluster groupings based on taxa similarity. Since stations varied in spatial coverage from year to year, GIS was used to determine the area of maximum spatial overlap of stations across years (2009 to 2010 and 2012 to 2013). The Generate Near Table tool was used to determine which stations were closest to one another among the year pairs, and the Join Field tool was used to determine the proximity by year. The CLUSTER analysis was rerun on the stations with maximum overlap to ensure the pattern seen was not due to the spatial mis-match among study years. Total community abundance and biomass distributions were calculated and visually represented through ArcGIS, and the means of each year were compared using an ANOVA test in R based on arcsine root transformed total abundance and biomass values to see if differences between years were statistically significant. All stations sampled in each year were used as replicates for that particular year. A Tukey test was then run to determine which years were significantly different from one another. Finally, to examine the amount of separation between years, an ANOSIM test in PRIMER was run on total biomass and abundance of the spatially overlapping stations. The R values, or the measure of scaled separation between groups, were compared.

To determine which specific taxa were responsible for differences in community composition between years, a SIMPER test in PRIMER was run on a Bray-Curtis similarity matrix on 4^{th} root transformed data to determine which taxa contributed to the differences among clusters and years for the spatially overlapping stations. An ANOVA test in R was performed on arcsine transformed relative biomass and abundance to see if proportions of major taxa varied significantly from 2009 to 2013 using the subset of spatially overlapping stations. Since proportional data have a binomial distribution, an arcsine transformation was used to standardize the data. A Tukey test was then performed to determine which years were statistically different from one another.

The temporally variable environmental drivers (bottom water temperature, salinity, dissolved oxygen, sediment grain size, C:N, and sediment chlorophyll *a* content) that were concurrently sampled at each station were normalized in PRIMER so drivers at a range of scales could be compared, and would contribute equally to the analysis. Collinearity between drivers was visually inspected using a Draftman's plot in PRIMER. If two drivers were found to be

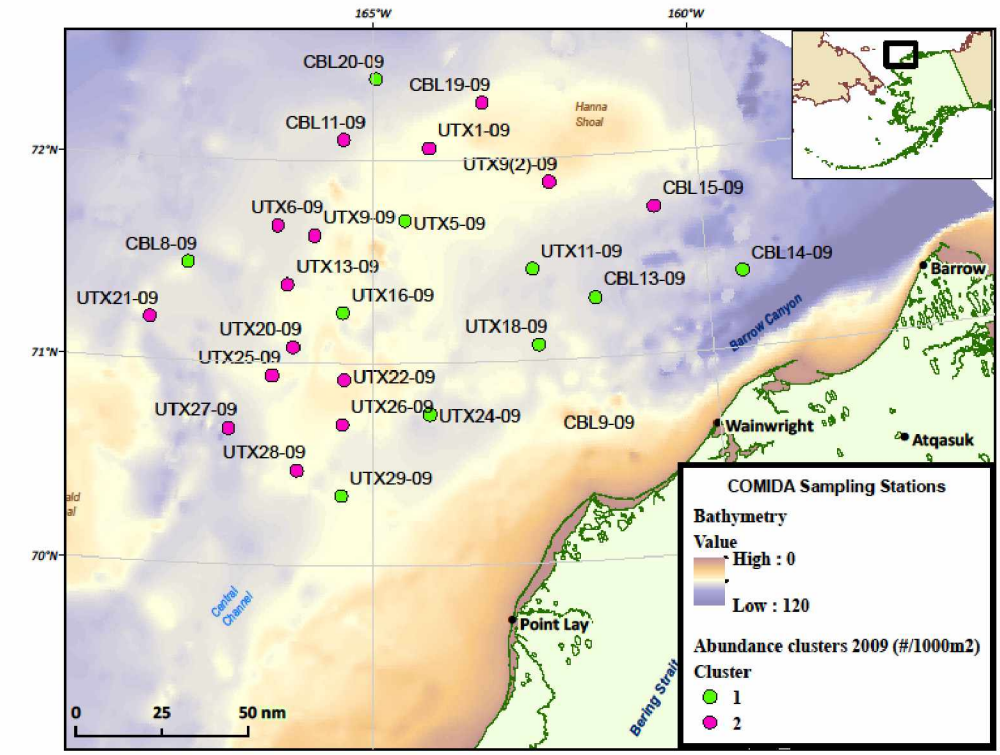
correlated at 90% or greater, determined by the underlying correlation matrix of the Draftman's plot, one was removed from further analysis. Conductivity was correlated with salinity and was therefore removed analysis. In addition, the various grain sizes of sand, mud and gravel (coarse, fine, very fine) all correlated with one another, and, therefore, percent mud was used as the sediment grain size variable. A Euclidean distance similarity matrix was then created on normalized environmental drivers. The BIO-ENV analysis in PRIMER was run to determine if any environmental drivers might be responsible for differences in epibenthic community structure for each year. This was done by comparing the Bray-Curtis and Euclidean distance resemblance matrices of the biological and environmental data, respectively, to determine if any environmental drivers correlated with the biological communities across the study region. This test was once again repeated on the subset of spatially overlapping stations to ensure that the observed pattern was not driven by a mis-match in spatial coverage between years.

3. Results

3.1 Abundance

Based on abundance of epibenthic communities, all stations in 2009 clustered into two groups at 80% similarity (Figure 2). Group 1, consisting of ten of the total 26 stations (in green), was primarily characterized by Ophiuroidea (90% of the total trawl abundance). Group 2, containing 15 stations (in pink), was dominated by *Chionoecetes opilio*, and secondarily by *Pagurus* spp. and Caridea (32%, 20%, and 16% of total abundance, respectively). There was also one unique station, CBL 9, which was located very close to shore and was composed mostly of the sand dollar *Echinarachnius parma* (95% of total abundance). Stations in 2010 grouped into three clusters at 80% similarity (Figure 3), which increased overall community complexity compared with 2009. Group 1, consisting of ten of the 24 stations (in pink), was dominated by Ophiuroidea with a secondary contribution by Caridea (61% and 15% of the total trawl abundance, respectively). Group 2, containing 14 stations (in green), was dominated primarily by Caridea (51% of the total trawl abundance), and secondarily by *C. opilio* and *Pagurus* spp. (20% and 14%, respectively). Lastly, group 3, consisting of two stations (in blue), was primarily composed of Ophiuroidea (69% of the total trawl abundance), with a 30% contribution of "others", which for UTX19 consisted of various gastropods, whereas WR1 had a large contribution from *Ocnus glacialis*. In the later years of the study, stations in 2012 clustered

together in two groups at 80% similarity (Figure 4). Group 1, containing 16 stations (in green), was dominated by Ophiuroidea with a secondary contribution by Caridea (60% and 20% of total abundance, respectively). Group 2, consisting of four stations (in pink), was dominated by Caridea (65% of the total trawl abundance), and secondarily by "others", which consisted of *Hyas coarctatus* and various gastropods (26% of the total abundance). Stations in 2013 grouped together in two clusters, also at 80% similarity (Figure 5). Group 1, containing 16 of the total 19 stations (in green), were dominated by Ophiuroidea and "others", which included various gastropods (47% and 23% of the total abundance, respectively). There was also a 17% contribution from Caridea. Group 2, consisting of three stations (in pink), contained primarily Caridea (75% of the total trawl abundance). Note that the same cluster numbers and colors among years (Figures 2-5) do not indicate any relationship between clusters in different years. In addition, the cluster analysis was repeated on the subset of stations that overlapped spatially, and resulted in the same overall pattern for each year: one cluster composed mostly of Ophiuroidea, and the other dominated by an arthropod (*C.opilio, Pagurus* spp., or Caridea).



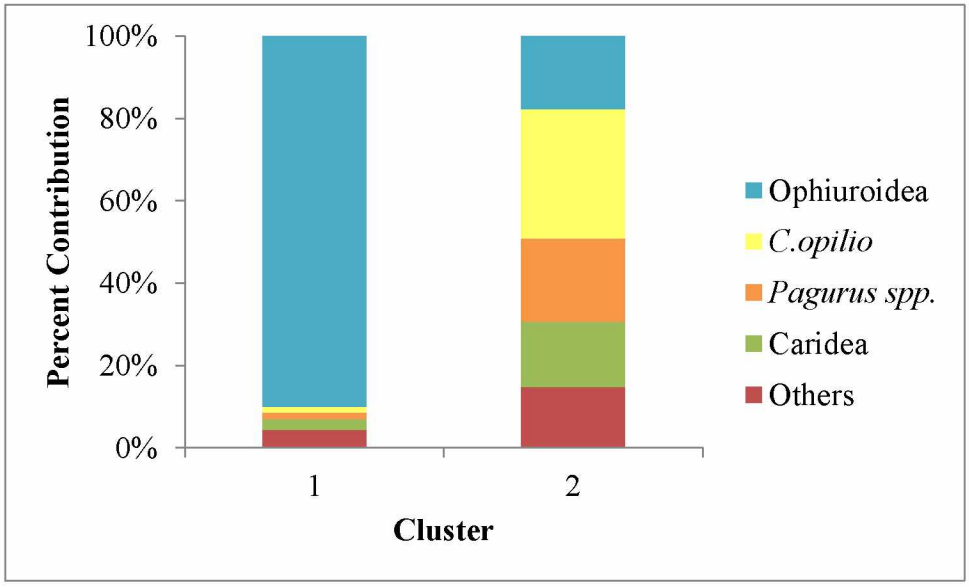


Figure 2: Epibenthic community composition based on abundance in 2009. Top: Stations clustered into two epibenthic communities at 80% similarity, shown in green (cluster 1) and pink (cluster 2). Bottom: Percent composition of the major taxonomic groups in clusters 1 (green) and 2 (pink).

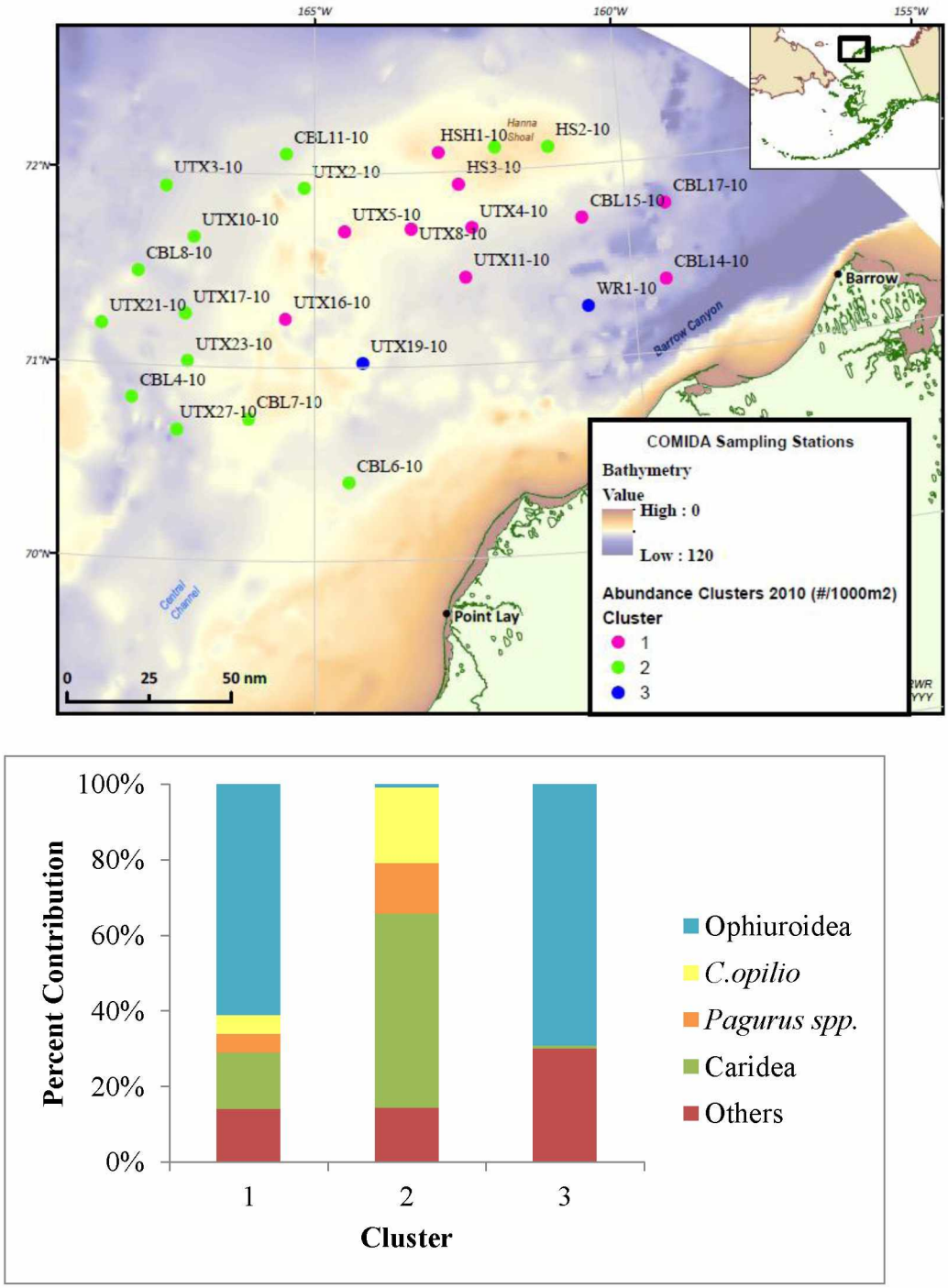


Figure 3: Epibenthic community composition based on abundance in 2010. Top: Stations clustered into three epibenthic communities at 80% similarity, shown in green (cluster 1), pink (cluster 2), and blue (cluster 3). Bottom: Percent composition of the major taxonomic groups in clusters 1 (green), 2 (pink), and 3 (blue).

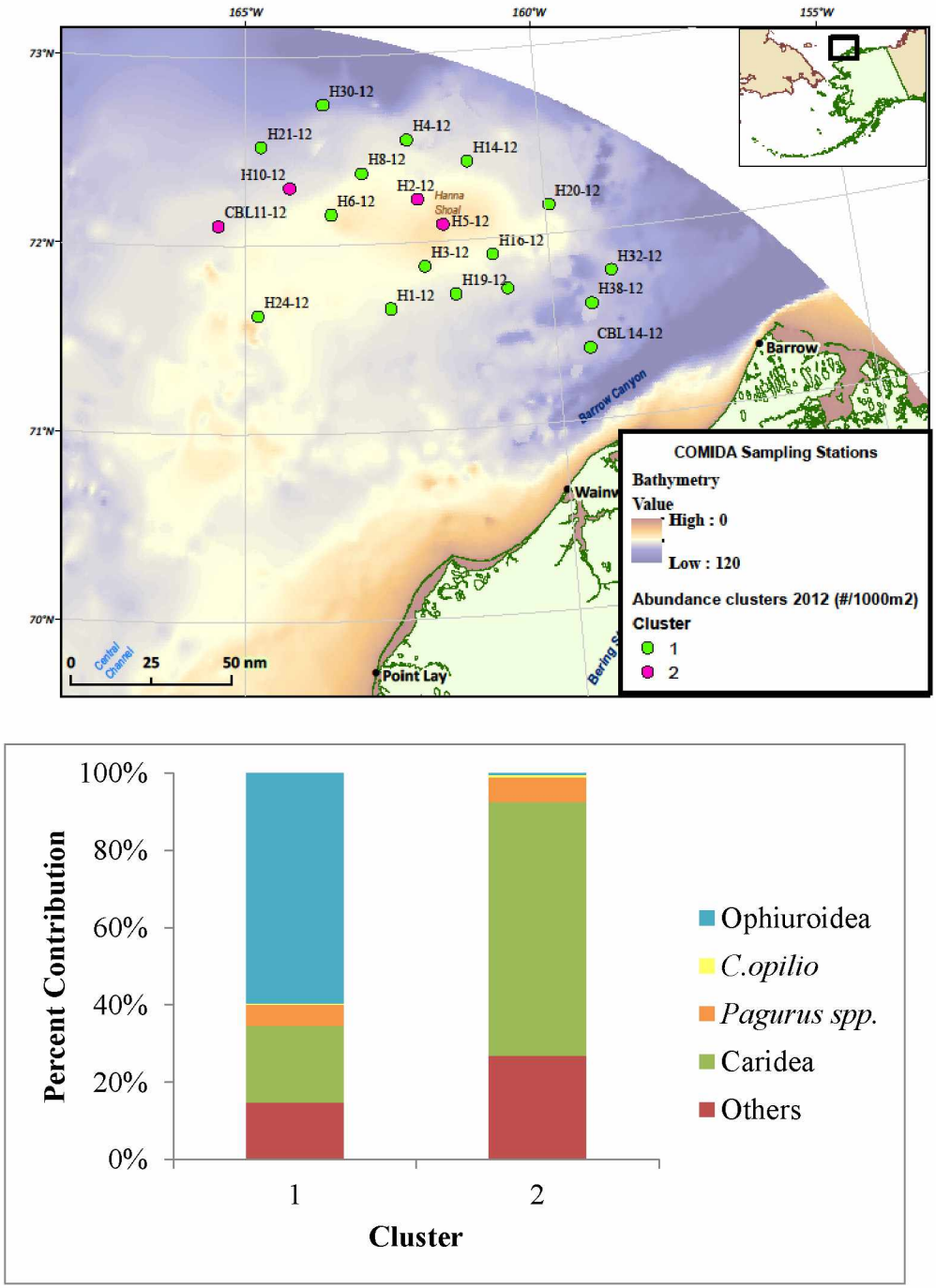


Figure 4: Epibenthic community composition based on abundance in 2012. Top: Stations clustered into two epibenthic communities at 80% similarity, shown in green (cluster 1) and pink (cluster 2). Bottom: Percent composition of the major taxonomic groups in clusters 1 (green) and 2 (pink).

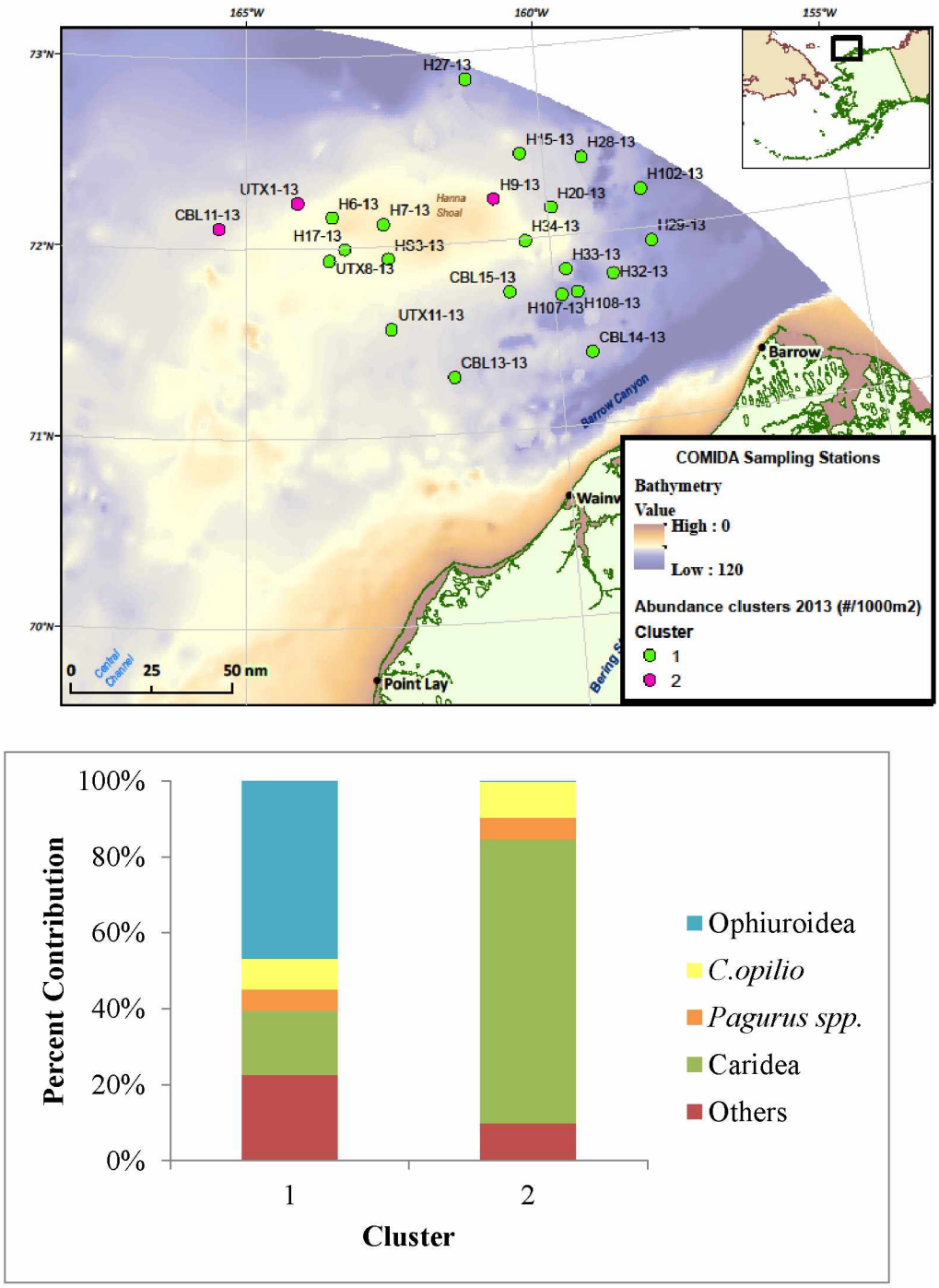


Figure 5: Epibenthic community composition based on abundance in 2013. Top: Stations clustered into two epibenthic communities at 80% similarity, shown in green (cluster 1) and pink (cluster 2). Bottom: Percent composition of the major taxonomic groups in clusters 1 (green) and 2 (pink).

Based on the subset of stations with the maximum spatial overlap (Figure 6), there was an overall decrease in mean abundance from year to year (Figure 7, Table 1). Stations sampled in 2009 had a mean abundance of 11,285±1,214 individuals per 1000 m^2 with the highest values at stations in the west of the study region. Stations in 2010 had a mean value of 6,863±4,061 individuals per 1000 m^2, with highest values in the south of the study region (Figure 7, Table 1). Stations sampled in 2012 and 2013 showed an overall drop in abundance from previous years with means of 3,661±1,500 and 444±200 individuals per 1000 m^2, respectively. Stations in each of these years (2012 and 2013) had a more uniform abundance distribution over the entire study area (Figure 7). The yearly abundances were significantly different between all individual years and 2013 (Table 1). Higher separation in abundance was observed between the earlier years (2009 and 2010) than between the later years (2012 to 2013), however these values are low and there is therefore little difference between these two year groups (ANOSIM; R= 0.082 and 0.029 for 09-10 and 12-13, respectively; Table 2). The most separation was found between 2009 and 2013, and the least from 2010 and 2013 (R= 0.277 and 0.009 for 09-13 and 10-13, respectively; Table 2).

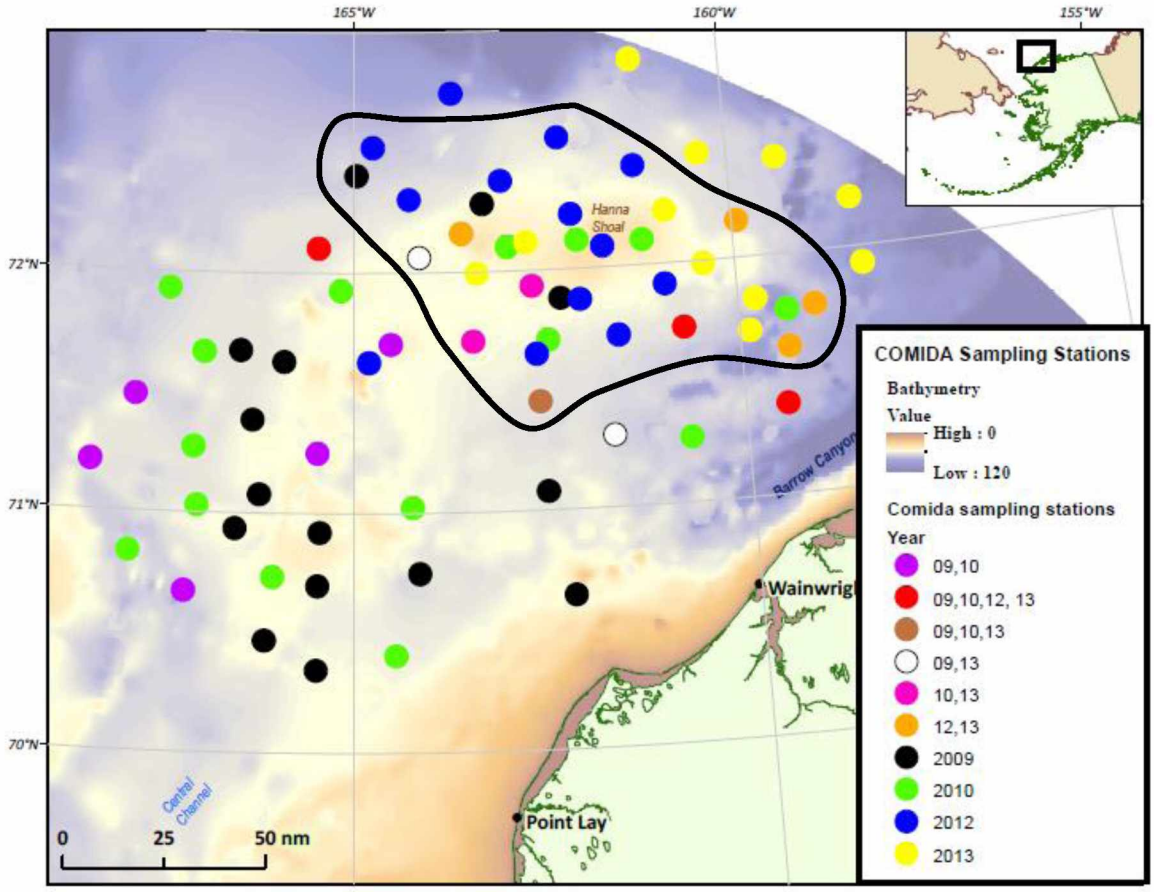


Figure 6: Circled stations are a subset of stations with the maximum spatial overlap for all years based on ArcGIS spatial analysis. Colors represent the sampling year.

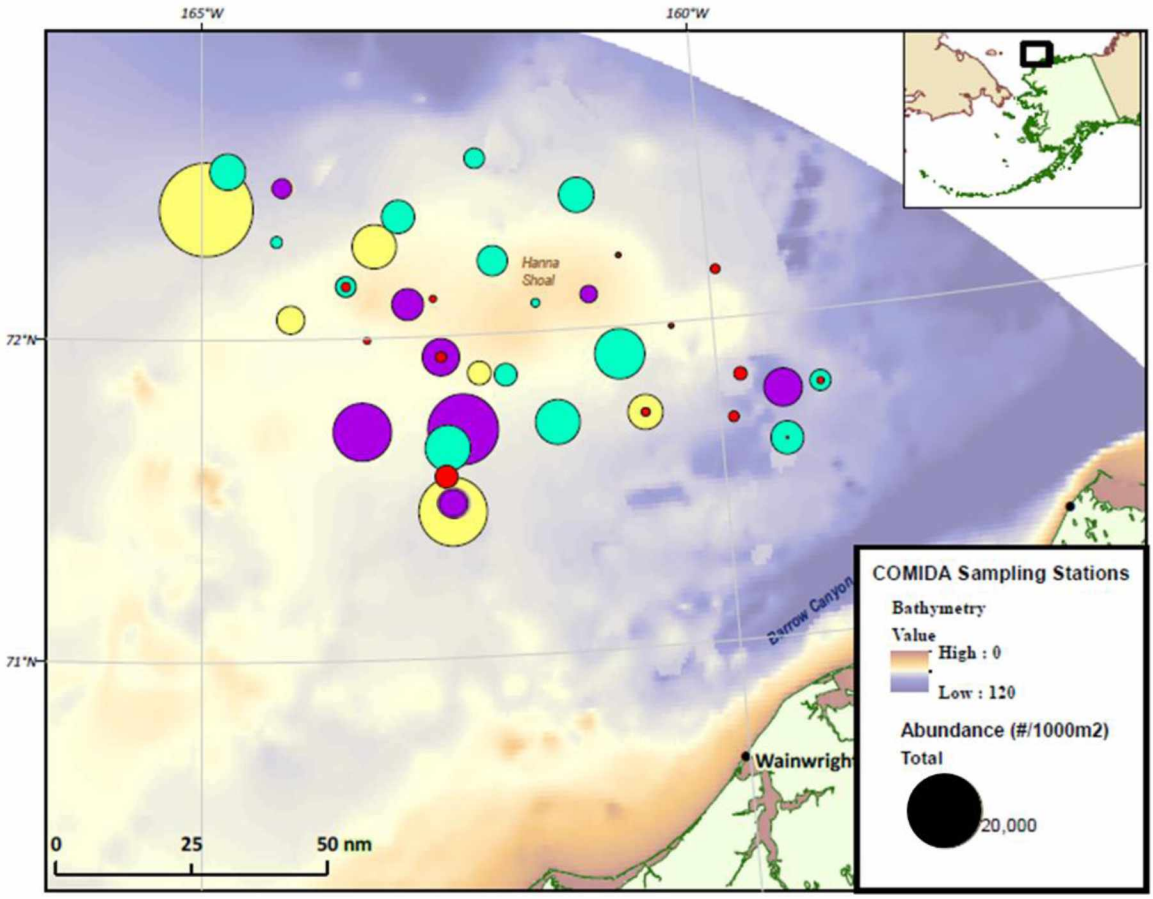


Figure 7: Total abundance of epibenthic communities from stations sampled in 2009, 2010, 2012, and 2013. Yellow circles represent stations sampled in 2009, purple circles 2010, teal circles 2012, and red circles 2013. Size of the circle indicates number of individuals.

Table 1: Top: One-way analysis of variance (ANOVA) and mean values and standard deviations in each year for total abundance and biomass within spatially overlapping stations. Asterisks represent statistically significant changes in total abundance and biomass over time. Bottom: Tukey test p-values for spatially overlapping stations of statistically significant differences in years. Asterisks represent statistically significant changes in total abundance and biomass over time.

	Sum of Squares	Mean Square	F-value	p-value	Mean 2009	Mean 2010	Mean 2012	Mean 2013
Abundance (#/1000m^2)	43.975	43.975	27.840	4.321e-06*	11,285± 1,1214	6,863± 4,061	3,661± 1,500	444± 200
Biomass (kg/1000m^2)	39.950	39.950	52.909	5.914e-09*	35±11	18±5	9±4	0.5± 0.2

	10 – 09	12 – 9	13 – 9	12 – 10	13 – 10	13 – 12
Abundance	0.563	0.00043*	3.12e-05*	0.098	0.00022*	0.0138*
Biomass	0.237	4.81e-05*	1.78e-06*	0.008*	0.0478*	0.0029*

Table 2: R-values, or the scaled degree of separation between years, based on the analysis of similarity (ANOSIM) test for epibenthic abundance and biomass.

	Years	**R-value**
Abundance	09-10	0.082
	09-12	0.111
	09-13	0.277
	10-12	0.033
	10-13	0.009
	12-13	0.029
Biomass	09-10	-0.058
	09-12	0.144
	09-13	0.275
	10-12	0.121
	10-13	0.184
	12-13	-0.075

For all years, four taxa best described overall epibenthic community abundance: the brittle star class Ophiuroidea, the snow crab *Chionoecetes opilio*, the hermit crabs *Pagurus* spp., and the infraorder of shrimp Caridea (SIMPER analysis, Spearman coefficient = 0.753, 0.818, 0.709, and 0.639 for 2009, 2010, 2012, and 2013, respectively). For subsequent analyses, all other taxa were included in the "others" category, and consisted of various gastropods, sea stars, bryozoans, the crab *Hyas coarctatus*, and the sea cucumber *Ocnus glacialis*. While the aforementioned groups were always the dominant taxa, the relative contribution of each group to total abundance varied significantly between years (Table 3-4). In 2009 and 2010, the majority of the community was composed of Ophiuroidea (Figure 2-3). However, between 2009 and 2010, *Chionoecetes opilio* contributed most to the separation in total abundance between years (Table 3-4). *Chionoecetes opilio* was a major contributor to abundance in 2009 and 2010, but not in 2012 and 2013, when the major contributor to total abundance were Caridea and *Pagurus* spp. In 2012, the majority of the community was composed of Ophiuroidea and Caridea (Figure 4). In 2013, Caridea and Ophiuroidea contributed most to community abundance, and Caridea contributed most to the separation between the years 2012 and 2013 (Figure 4-5). Out of the major taxa describing the community, *C. opilio* decreased significantly in abundance across most year pairs, while *Pagurus* spp. increased significantly from 2009 to 2013 ($p = <0.001$ and 0.004, respectively; Table 3-4). Specifically, *C. opilio* abundances were significantly different between the years 2009 and 2012, 2009 and 2013, and 2010 and 2012 (Table 3). For *Pagurus* spp., however, the only significant differences in abundance were between 2009 and 2012 and between 2009 and 2013 (Table 3).

Table 3: Top: One-way analysis of variance (ANOVA) of major taxa based on relative abundance and biomass within spatially overlapping stations by year. Asterisks represent statistically significant changes in taxon abundances over time. Bottom: Tukey test p-values for spatially overlapping stations of taxa with statistically significant differences in years: *C.opilio*, *Pagurus* spp., and Caridea

	Major Taxa	**Sum of squares**	**Mean square**	**F-value**	**p-value**
Abundance	Ophiuroidea	<0.001	<0.001	<0.001	0.994
	Chionoecetes opilio	0.277	0.277	13.45	<0.001*
	Pagurus spp.	0.070	0.070	8.788	0.004*
	Caridea	0.160	0.160	2.040	0.157
	Others	0.068	0.068	1.989	0.162
Biomass	Ophiuroidea	0.425	0.425	3.163	0.079
	Chionoecetes opilio	1.864	1.864	32.54	<0.001*
	Pagurus spp.	0.006	0.006	0.519	0.473
	Caridea	0.052	0.052	8.686	0.004*
	Neptunea spp.	<0.001	<0.001	0.394	0.532
	Others	0.170	0.170	3.055	0.084

Taxa	**Year**					
	10 – 09	**12 – 09**	**13 – 09**	**12 – 10**	**13 – 10**	**13 – 12**
Abundance						
C.opilio	0.433	<0.001*	0.050*	0.008*	0.660	0.153
Pagurus spp.	0.640	0.058	0.054*	0.544	0.519	0.999
Biomass						
C.opilio	0.965	<0.001*	<0.001*	<0.001*	<0.001*	0.999
Caridea	0.436	0.032*	0.029*	0.513	0.522	0.999

Table 4: Mean values for relative abundance and biomass for taxa that varied significantly between 2009, 2010, 2012, and 2013.

Organism	**Year**			
	2009	**2010**	**2012**	**2013**
Abundance				
Chionoecetes opilio	0.286±0.192	0.126±0.091	0.002±0.001	0.087±0.025
Pagurus spp.	0.122±0.095	0.092±0.072	0.056±0.028	0.055±0.037
Biomass				
Chionoecetes opilio	0.331±0.116	0.317±0.105	0.053±0.021	0.036±0.011
Caridea	0.011±0.001	0.044±0.005	0.098±0.020	0.168±0.053

The environmental drivers that best explained the patterns in community structure varied over time. In 2009, sediment grain size best matched the biological community patterns (BIO-ENV analysis, $\rho = 0.576$). In 2010, sediment grain size, salinity, the C:N ratio within the sediment, and dissolved oxygen ($\rho = 0.439$) were the most important drivers. In 2012, four drivers were also important but in this year, they were sediment grain size, salinity, the C:N ratio within the sediment, and bottom temperature ($\rho = 0.481$). Finally, 2013 also indicated four important drivers: sediment grain size, the percentage of carbon to nitrogen, temperature, and mean sediment chlorophyll *a* ($\rho = 0.520$). Overall, sediment grain size was important in all years. Dissolved oxygen was only important in 2009, whereas mean sediment chlorophyll was only important in 2013. Temperature became important in the later years of the study (2012 and 2013). The C:N ratio within the sediment was important in all years except 2009, and salinity was only important in 2010 and 2012. These patterns held true when community patterns were analyzed over all stations within the study area, as well as when only the stations with the maximum spatial overlap were considered. This suggests that the spatial mis-match in station location across years did not contribute to the selection of important environmental drivers.

3.2 Biomass

Based on epibenthic community biomass composition, all of the 2009 stations grouped into two clusters with 80% similarity (Figure 8). Group 1, consisting of 12 of the total 26 stations (in green), was dominated by Ophiuroidea (65% of the total trawl biomass), and secondarily by "others" and *Chionoecetes opilio* (17% and 12%, respectively). "Others" consisted of various gastropods and sea stars. Group 2, consisting of 13 stations (in pink), was characterized mainly by *C. opilio* with a secondary contribution of *Pagurus* spp. and "others", which were various gastropods, sea stars, and the anemone *Stomphia* spp. (17%, 51%, and 19%, of the total biomass, respectively). There was also one unique station, CBL 9, located very close to shore. Similar to abundance, this station was dominated by *Echinarachnius parma* (96% of the total trawl biomass). In 2010, stations grouped together in three clusters, at 80% similarity (Figure 9), which increased overall community complexity in this year. Group 1, containing ten of the total 24 stations (in green), was dominated by Ophiuroidea with a secondary contribution by "others", which were various gastropods and *C. opilio* (49%, 23%, and 16% of the total biomass, respectively). Group 2, consisting of 11 stations (in pink), was dominated by *C. opilio* (64% of the total trawl biomass) and secondarily by *Pagurus* spp. and "others", which were various gastropods and *Gersemia* spp. (20% and 11%, respectively). Group 3, containing the final three stations (in blue), was characterized by "others", which were primarily gastropods and bryozoans, and had secondary contributions from both *C. opilio* and Caridea (44%, 24%, and 23%, respectively). There were also two unique stations that did not group with other stations, UTX19 and WR1. UTX19 was mostly composed of the sea star *Leptasterias* spp. and various gastropods (41% and 35%, respectively), whereas WR1 consisted primarily of *Ocnus glacialis* (81% of total trawl biomass). Stations in 2012 clustered together into two groups at 80% similarity (Figure 10). Group 1, consisting of 14 of the total 20 stations (in green), was comprised mostly of Ophiuroidea, with a small contribution from "others", which were various sea stars, bryozoans and *Hyas coarctatus* (62% and 18% of the total biomass, respectively). Group 2, containing four stations (in pink), was dominated by "others", which were various gastropods, and secondarily *Pagurus* spp. and Caridea (48%, 18%, and 11%, respectively). There were also two unique stations, CBL11 and H5. CBL11 was dominated by various gastropods, and H5 was dominated by the bryozoan *Alcyonidium disciforme* (50% of total trawl biomass). In 2013, stations clustered into two groups, also at 80% similarity (Figure 11). Group 1, consisting

of 18 of the total 23 stations (in green), was comprised mostly of Ophiuroidea and "others", which were various sea stars (52% and 30% of total trawl biomass, respectively). Group 2, consisting of five stations (in pink), was comprised primarily of "others", in this case the sea star *Ctenodiscus crispatus* (44% of the total trawl biomass), and secondarily *Pagurus* spp., Caridea, and *C. opilio* (20%, 19%, and 12%, respectively). Note that the same cluster numbers and colors among years (Figures 8-11) do not indicate any relationship between clusters in different years. When biomass from the subset of stations with the maximum spatial overlap across years was examined, the same pattern was observed; one cluster was composed mostly of Ophiuroidea, and the other was dominated by an arthropod (*C.opilio, Pagurus* spp., or Caridea).

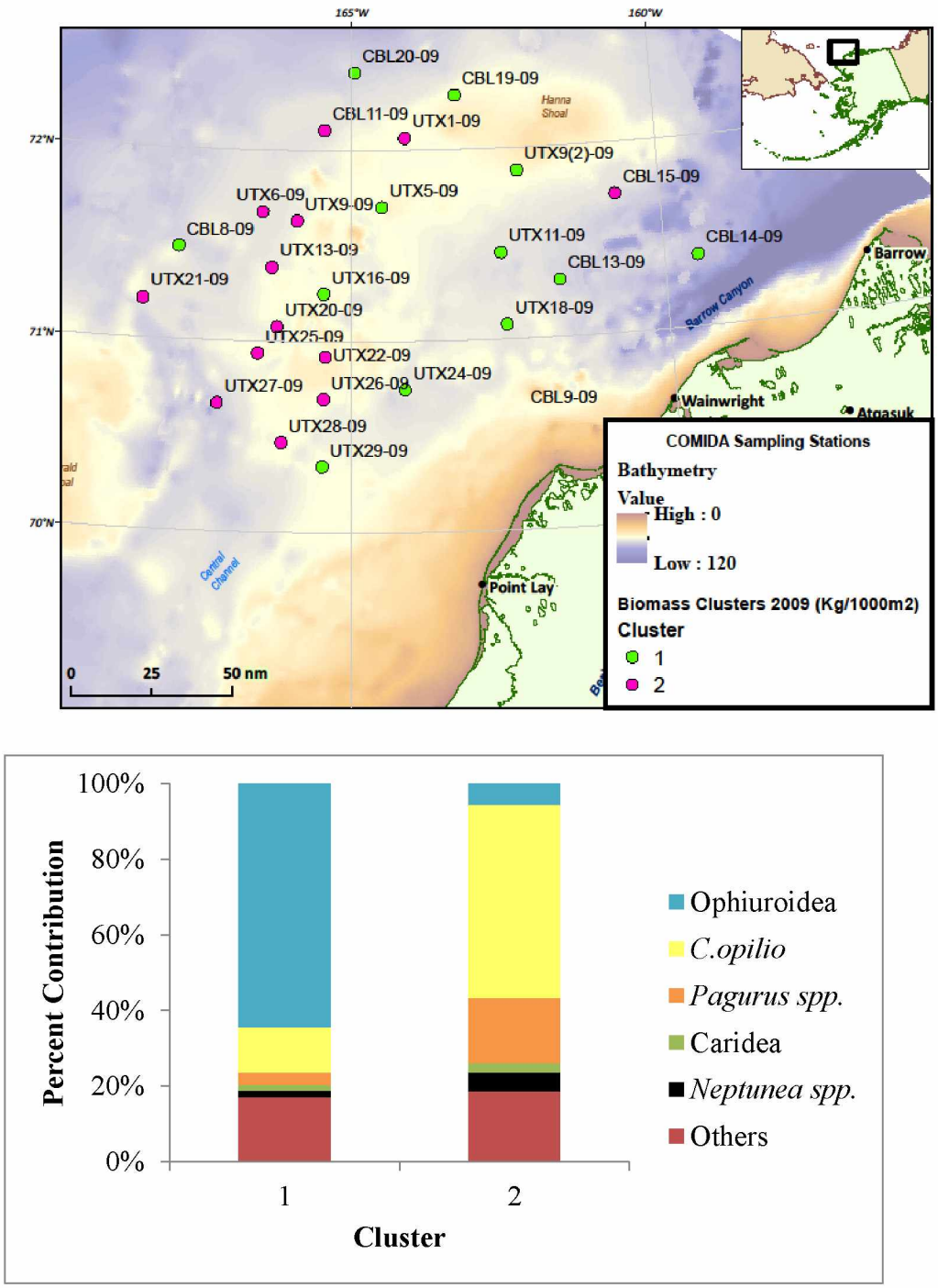


Figure 8: Epibenthic community composition based on biomass in 2009. Top: Stations clustered into two epibenthic communities at 80% similarity, shown in green (cluster 1) and pink (cluster 2). Bottom: Percent composition of the major taxonomic groups in clusters 1 (green) and 2 (pink).

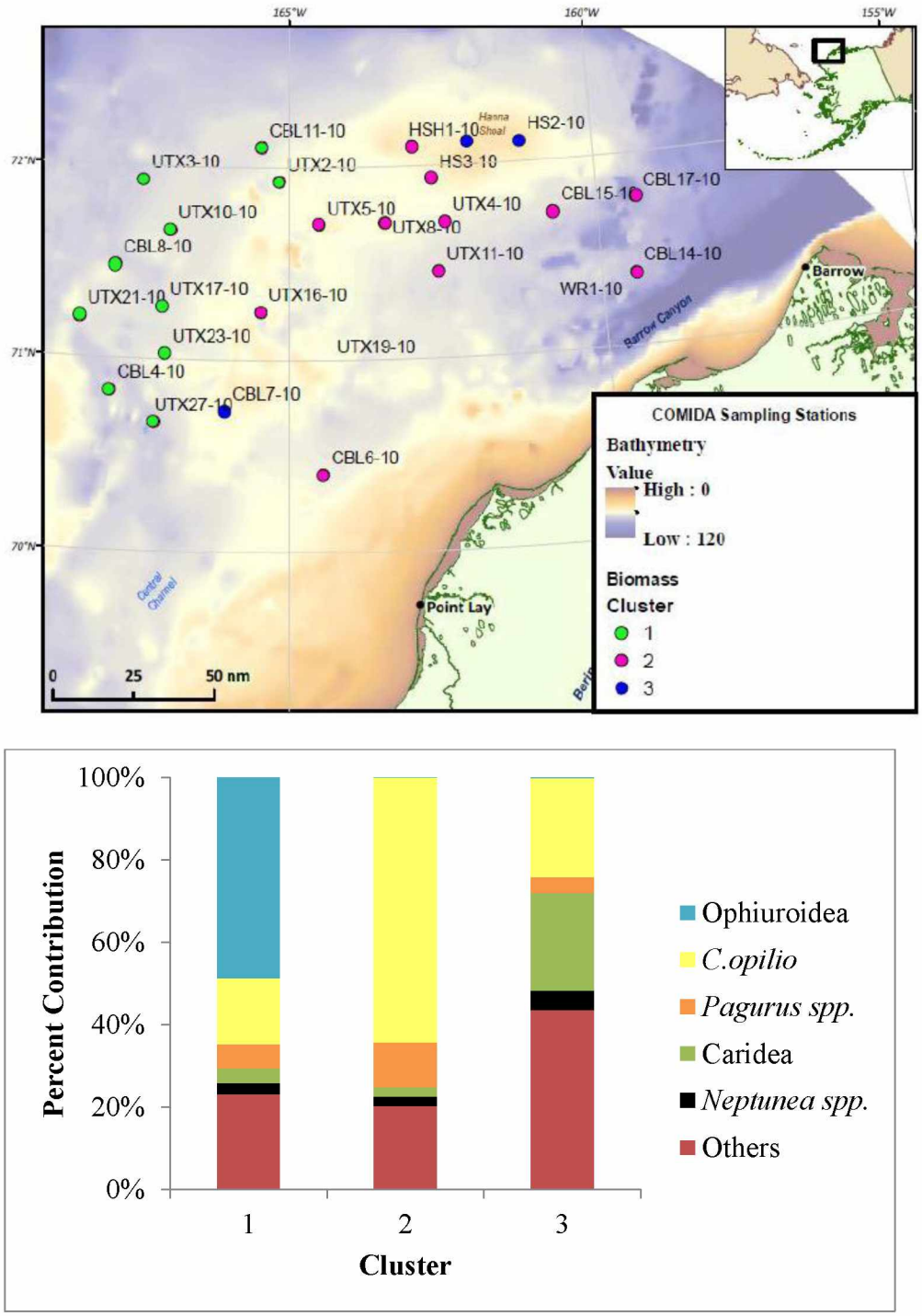


Figure 9: Epibenthic community composition based on biomass in 2010. Top: Stations clustered into three epibenthic communities at 80% similarity, shown in green (cluster 1), pink (cluster 2), and blue (cluster 3). Bottom: Percent composition of the major taxonomic groups in clusters 1 (green), 2 (pink), and 3 (blue).

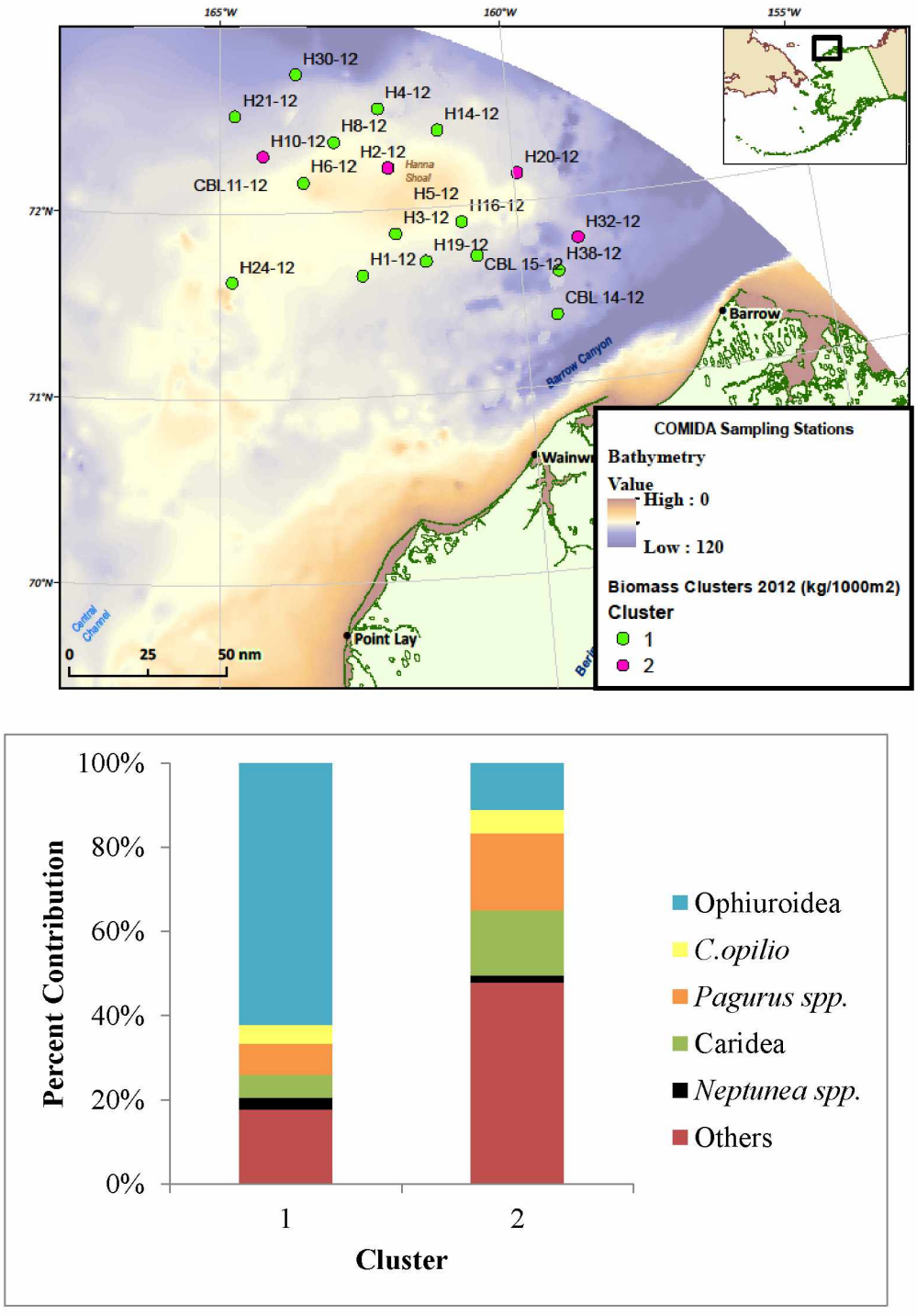
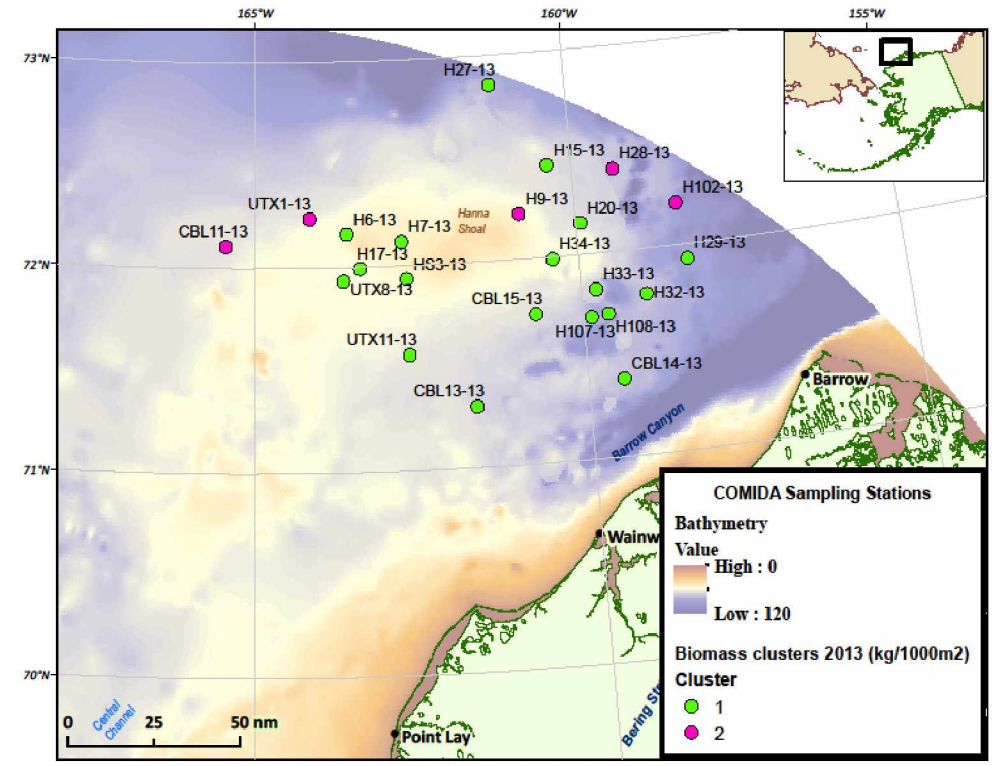


Figure 10: Epibenthic community composition based on biomass in 2012. Top: Stations clustered into two epibenthic communities at 80% similarity, shown in green (cluster 1) and pink (cluster 2). Bottom: Percent composition of the major taxonomic groups in clusters 1 (green) and 2 (pink).



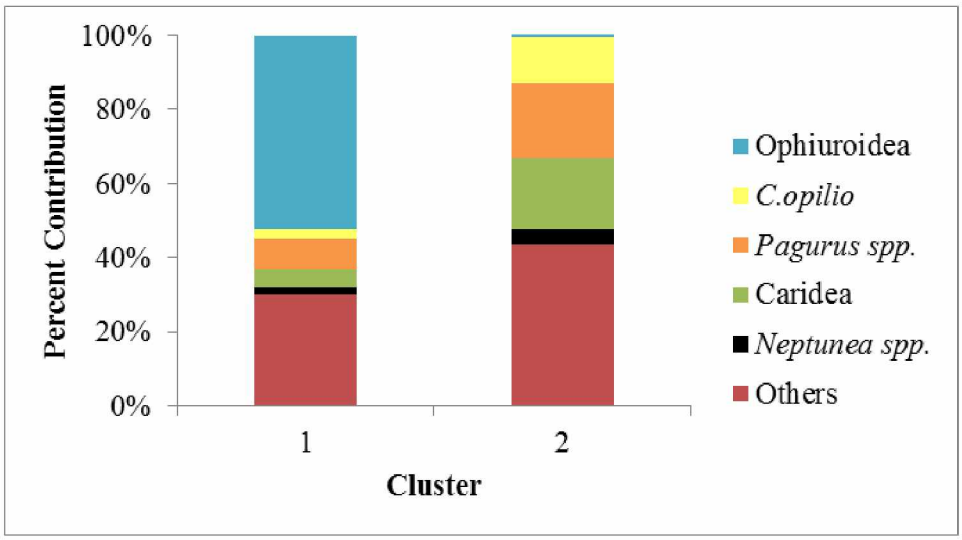


Figure 11: Epibenthic community composition based on biomass in 2013. Top: Stations clustered into two epibenthic communities at 80% similarity, shown in green (cluster 1) and pink (cluster 2). Bottom: Percent composition of the major taxonomic groups in clusters 1 (green) and 2 (pink).

There was a decrease in mean biomass from year to year based on the subset of maximum overlap stations (Figure 12, Table 1). Stations in 2009 had a mean biomass of 35±11 kg wet weight per 1000 m^2 with the highest biomass located in the western study area. Mean biomass in 2010 was 18±5 SD kg wet weight per 1000 m^2, with the largest biomass values to the southwest (Figure 12, Table 1). There was an overall decrease in biomass in 2012 and 2013, with mean values of 9±4 kg wet weight per 1000 m^2 and 0.5±0.2 kg wet weight per 1000 m^2, respectively (Figure 12, Table 1). In these latter years, biomass was more evenly distributed across stations. The yearly biomass values were significantly different between 2013 and all other years, as well as between 2010 and 2012 (Table 1). Based on biomass, there was no difference in community structure between 2009-2010 and between 2012 and 2013, since negative R-values are considered zero. More separation in communities based on biomass was seen between 2009 and 2010 than between 2012 and 2013 (R = -0.058 and -0.075 for 09-10, and 12-13 respectively; Table 2). Based on the stations with maximum spatial overlap, the most separation was found between 2009 and 2013, and the least between 2009 and 2010 as well as between 2012 and 2013 (R = 0.275, -0.058, and -0.075 for 09-13, 09-10, and 12-13, respectively; Table 2). Furthermore, in the later years of the study, biomass was more uniformly distributed over the entire study area as opposed to 2009 and 2010, when it was more variable (Figure 12).

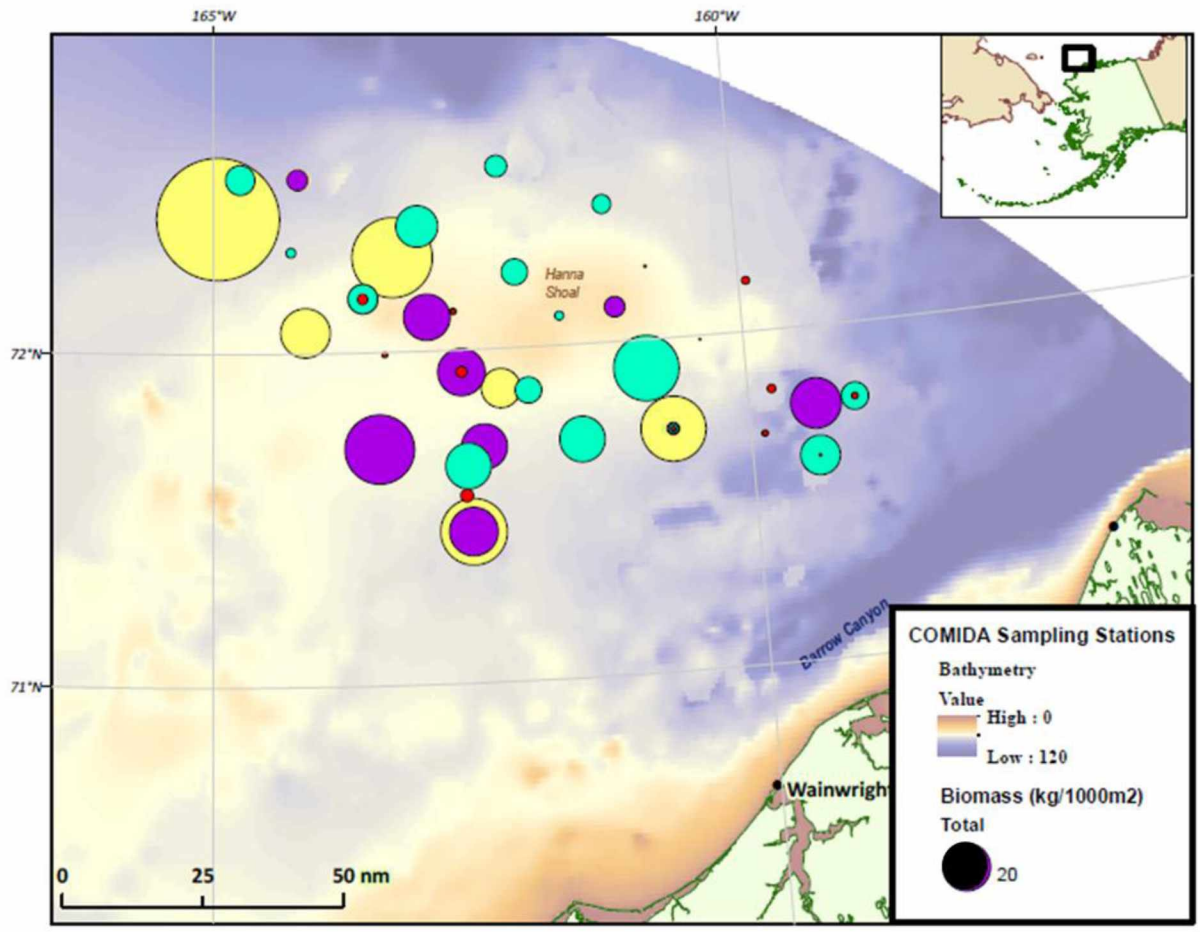


Figure 12: Total biomass of epibenthic communities from stations sampled in 2009, 2010, 2012, and 2013. Yellow circles represent stations sampled in 2009, purple circles 2010, teal circles 2012, and red circles 2013. Size of the circle indicates kg wet weight.

Five taxa best described overall epibenthic community biomass for all years: Ophiuroidea, *Chionoecetes opilio*, *Pagurus* spp., Caridea, and the large predatory gastropod *Neptunea* spp. (SIMPER analysis, Spearman coefficient = 0.745, 0.783, 0.751, and 0.649 for 2009, 2010, 2012, and 2013, respectively). All other taxa were included in "others", which was defined as various gastropods, sea stars, bryozoans, the soft coral *Gersemia* spp., the crab *Hyas coarctatus*, the anemone *Stomphia* spp., and the sea cucumber *Ocnus glacialis*. The "dominant" groups mentioned above did not differ among years; however, the relative contribution of each group to toal biomass (the difference seen in the percent biomass) varied significantly between

years (Table 3-4). In 2009, the majority of the community was composed of Ophiuroidea and *C. opilio* (Figure 8). Between 2009 and 2010, *C. opilio* contributed most to the separation between years (Table 3-4). Stations sampled in 2010 were composed mainly of *C. opilio,* but both *C. opilio* and Ophiuroidea contributed most to the separation between years (Figure 9). *Chionoecetes opilio* was a major contributor to biomass in 2009 and 2010, and Caridea and *Pagurus* spp. were the major biomass contributors in 2012 and 2013. In 2012 and 2013, the majority of the community was composed of Ophiuroidea (Figure 10-11). Between 2012 and 2013, *C. opilio* and Caridea contributed most to the separation between years (Table 3-4). Of the major taxa that described the community, only *C. opilio* and Caridea varied significantly over the four years of the study ($p = 1.37e-07$ and 4.05e-03, respectively; Table 3-4). The proportion of *C. opilio* significantly decreased across most year pairs, whereas Caridea significantly increased from 2009-2012 and 2009-2013 (Table 3-4). Specifically, *C. opilio* biomass was significantly different between the years 2009 and 2012, 2009 and 2013, 2010 and 2012, and between 2010 and 2013 (Table 3). For Caridea, however, the only significant differences were between 2009 and 2012, and 2009 and 2013 (Table 3).

The environmental drivers that best matched the biological community patterns changed over the study years. In 2009, it was sediment grain size (BIO-ENV analysis, $\rho = 0.618$), while in 2010, they were sediment grain size, salinity, the C:N ratio within the sediment, and dissolved oxygen ($\rho = 0.488$). For 2012, sediment grain size, salinity, the C:N ratio within the sediment, and temperature were most important ($\rho = 0.532$), while in 2013, sediment grain size, the C:N ratio, temperature, and mean sediment chlorophyll *a* had the highest correlation to epibenthic community patterns ($\rho = 0.451$). Overall, sediment grain size was important in all years. In contrast, dissolved oxygen and mean sediment chlorophyll *a* were only important in 2010 and 2013 respectively. Temperature became important in the last two years of the study. The C:N ratio within the sediment was important in 2010, 2012 and 2013. The environmental drivers best matching community biomass variability were the same when analyzed over all stations, or when only the stations with the maximum spatial overlap were considered. This suggests that the spatial mis-match in station location among years did not contribute to the selection of important environmental drivers.

4. Discussion

4.1 Community Composition Patterns

Epibenthic abundance, biomass, and community composition (primarily *Chionoecetes opilio, Pagurus* spp., and Caridea) were temporally variable across the Chukchi Sea study area. There was more separation in epibenthic community composition between 2009 and 2013 for both relative abundance and biomass. The least separation was found between 2010 and 2013 for abundance, and between 2009 and 2010 as well as 2012 and 2013 for biomass Station clusters in 2009 and 2010 contained relatively equal numbers of stations within two main clusters in each year (a small third cluster in 2010), whereas in 2012 and 2013, most stations grouped together into one large cluster with only three or four stations clustering separately. This could indicate that epibenthic communities were becoming more homogeneous and less complex, with a more equal species distribution.

Previous studies in the Chukchi Sea have shown a very productive and dynamic system with high abundance, biomass, and temporal as well as spatial variation of both epi- and infaunal communities (Grebmeier et al., 2006; Piepenburg, 2006; Ravelo et al., 2014). A so-called "hotspot" of benthic abundance and biomass exists southeast of Hanna Shoal (Grebmeier et al., 2006), where a convergence of currents increases deposition of organic matter to the epibenthic environment (Weingartner et al., 2013). High abundance and biomass was seen here in the epibenthic community in the first two years of this study; however, it was not seen in the last two years when abundance and biomass were very low. This holds true for all stations as well as the subset of spatially overlapping stations. The variation in hotspot abundance and biomass could be due to changes in current regimes, which may lead to a decrease in the amount of primary production reaching the seafloor. Another possibility is the regionally colder temperatures that have been observed in recent years, which could be due to slower flushing times of the cold dense winter water that forms on Hanna Shoal, which normally gets replaced by Bering Sea-Anadyr Water in early summer (Day et al., 2013). Colder temperatures are not favorable for several of the major epibenthic players in the Chukchi Sea, as colder temperatures have been found to inhibit larval recruitment and development (Ernst et al., 2005; Day et al., 2013; Balazy et al., 2015). Most studies focusing on variability in Arctic benthic communities have examined long term changes in abiotic drivers, such as sea ice cover and circulation patterns (Walsh, 1978;

Semtner Jr., 1987; Johannessen et al., 2004; Stroeve et al., 2007). The Chukchi Sea varies greatly in ice cover, circulation, temperature, salinity, and the amount of production sinking to the benthos from year to year (Grebmeier and Barry, 1991; Winsor and Chapman, 2002; Arrigo and van Dijken, 2004; Grebmeier et al., 2006). This current study agrees with past studies in that the Chukchi Sea is dynamic, and that the importance of environmental drivers of epibenthic communities varies by year. The important drivers of community structure in this study were pH, temperature, and the percentage of carbon to nitrogen within the sediment. This environmental variability probably influences interannual variability in the biological community.

Crustaceans contributed most to the temporal differences in community composition, whereas both crustaceans and echinoderms were the major contributors to total abundance and biomass across the study region in every year. One species, *Chionoecetes opilio* was particularly variable in abundance and biomass over time (Table 2-3). In addition, the sizes of *C. opilio* have also varied over spatial and temporal scales in this study area (Konar et al., 2014; Gross and Konar, unpublished data). Previous studies in the Bering Sea reported *C. opilio* migration patterns that would be reflected in abundance, biomass and size frequency patterns (Somerton, 1981a; Ernst et al., 2005). Bering Sea *C. opilio* can undergo ontogenetic migrations of 73.5 nautical miles from shallow to deeper water (Ernst et al., 2005); although traditionally, migrations have been regarded as negligible since only shorter migrations have been found (Somerton, 1981b; Incze et al., 1987). In the Bering Sea, eggs are hatched in shallow waters because these regions are suitable for the survival, retention, and settlement of pelagic larvae (Ernst et al., 2012). Juvenile crabs also tend to stay in shallow water because they prefer the increased dissolved oxygen associated with these depths (Dionne et al., 2003). Once they settle, crabs grow to maturity, mate, and migrate to deep water (Ernst et al., 2005; Parada et al., 2010). This shallow to deep migration cycle has been monitored for three decades in the Bering Sea, and appears to have a mean period of seven years per cohort (Ernst et al., 2012). The same migratory pattern/periodicity in cohort development could be happening in the Chukchi Sea, as evidenced by the variability in abundance and biomass over time, and the overall decrease in mean values of *C. opilio* in this current study. Migrations of *C. opilio* may be following environmental gradients. Bering Sea mature female *C. opilio* follow bottom temperature gradients and population movements are prevented by excessive cooling or heating of water, since crabs have preferred temperature ranges of 0-4.5^{0}C (Dionne et al., 2003; Ernst et al., 2005).

This observed temperature preference matches the present study, as temperatures above 0°C in 2009 and 2010, and temperatures below 0°C were observed for 2012 and 2013. If these temperature constraints are the same for Chukchi Sea crabs, mature crabs might migrate off the shelf onto the slope to find warmer water flowing in from the Atlantic, reaching 1°C at depth (Coachman and Barnes, 1963). Temperatures below 0°C are not suitable for adult crabs, and may help explain the decrease in abundance and biomass that was observed in the later two study years if the temperature point measurements are representative of a more permanent decrease of temperature in the region.

Colder water may also have implications for Caridea and *Pagurus* spp. as well. The proportion of shrimp biomass became higher from 2009 to 2013 and less variable over time. The Gulf of Alaska experienced a regime shift in 1977 from a cold to warm temperature regime, which negatively affected the pandalid shrimp population (Anderson, 2000; Hare and Mantua, 2000; Overland et al., 2008). Shrimp are ecologically important, since they can occupy all depths and are common in high latitude food webs (Anderson, 2000). In the late 1970s, warming in the Gulf of Alaska caused pandalid shrimp to rapidly decline in abundance (Anderson and Piatt, 1999; Anderson, 2000), as seen in the inverse relationship of temperature with shrimp recruitment (Anderson, 2000). In the northeastern Chukchi Sea, decreasing temperatures may thus support higher shrimp recruitment and may help explain the increase in shrimp biomass over the study years, if caridean shrimp in the Arctic exhibit a similar temperature preference as pandalid shrimp in the Gulf of Alaska. There have been very few studies on *Pagurus* spp. in the Arctic, but through the use of gastropod shells they not only provide transportation, but habitat for epibionts (Williams and McDermott, 2004; Balazy et al., 2015), and are, therefore, considered important ecosystem engineers (Balazy et al., 2015). In the laboratory, *Pagurus* spp. populations in northern Norway decreased with a decrease in temperature because lower temperatures inhibited larval development (Balazy et al., 2015). This temperature dependence could explain the observed decrease of *Pagurus* spp. abundance over time in the present study. Both Caridea and *Pagurus* spp. are important players in Arctic ecosystems, and therefore, variation in the abundance and biomass of these species will impact other trophic levels.

The variability in the epibenthic community observed in the current study has implications for higher trophic levels, such as benthic feeding marine mammals who utilize the

Chukchi Sea epibenthos as a prey source. For example, Hanna Shoal is a preferred feeding ground for walrus (Jay et al., 2012). Walrus rarely dive deeper than 100 m, so the shallow environment of the Chukchi Sea and specifically Hanna Shoal is ideal for walrus foraging (Fay, 1982; Moore and Huntington, 2008). In addition, there is a hotspot of benthic fauna on Hanna Shoal, where ice remains until late into the summer (Martin and Drucker, 2012). This is especially important for walrus, which utilize ice for resting between feeding bouts to conserve energy and maintain their blubber layer (Moore and Huntington, 2008). This current study found a decrease in epibenthic community complexity, abundance and biomass, especially in the later years of the study. If these trends continue and this is an actual decline and not just interannual variability, upper trophic levels that depend on the extensive epibenthic community could be impacted. It should be noted that these declines may simply be part of the natural variability in the system and more monitoring is needed to confirm this.

4.2 Environmental Analysis

The Chukchi Sea is a very dynamic ecosystem, with much variability in its environmental drivers along with its biological communities. The correlations of environmental drivers with biological communities were reasonably strong and demonstrated that most of the primary drivers (bottom water temperature, salinity, dissolved oxygen, mean sediment chlorophyll *a*, and sediment organic matter) differed over time. One exception was sediment grain size, which was an important driver for describing community composition in all years for both relative abundance and biomass. These environmental drivers are associated with hydrodynamic regimes (currents and water mass characteristics), which are known to vary across years in the Chukchi Sea (Weingartner et al., 1998; Winsor and Chapman, 2002; Weingartner et al., 2005).

Variability in hydrographic regimes (current and water mass properties) can cause shifts in the dominant epibenthic taxa. Sediment grain size and sediment quality characteristics are thought to be proxies for current features. Faster currents produce coarser sediment whereas slower currents create fine grained sediment habitats (Grebmeier et al., 1989). In addition, currents determine how much organic matter reaches the benthos. The Chukchi Sea current systems are highly variable and have been known to change direction with strong wind regimes, which can also vary interannually (Weingartner et al., 1998; 2005; 2013). For example, reversal of the Alaska Coastal Current would ultimately change the sediment grain size and the amount of

production reaching the benthos, which might impact the resident organisms (Blanchard et al., 2013a). Interannual variation in water mass characteristics is also high in the Chukchi Sea, with large differences in temperature and salinity between successive winters (Winsor and Chapman, 2002). Temperature and salinity define water masses, which subsequently can cause variation in the amount of productivity in the water column. A shift in temperature would cause zooplankton grazing rates to change, since as temperature increases or decreases so too does metabolism. A larger fraction of primary production retained in the pelagic system would subsequently affect the amount of primary production available to epibenthic organisms (Arrigo and van Dijken, 2004),. Density in high latitude systems is mostly driven by salinity, which influences deep water formation and therefore ventilation of benthic systems (Winsor and Chapman, 2002). Benthic biomass is two to ten times greater under the nutrient-rich Bering Shelf-Anadyr Water than it is under Alaska Coastal Water (Springer and McRoy, 1993; Blanchard and Feder, 2014). Therefore, the variability observed in the epibenthic community in the present study could have been due to a shift in current regime or water mass properties.

Bering Sea-Anadyr Water flows northward offshore, and splits around Hanna Shoal in the northeast. The upper arm of this split continues around the top of the shoal, and then wraps back on itself to meet up with the lower arm of the split, ultimately forming a convergence south of Hanna Shoal (Weingartner et al., 2005; 2013). This convergence allows for slower water motion, and thus retains a cold pool of winter water with a slow flushing of this water in the summer, when it is commonly replaced by Bering Shelf-Anadyr Water (Weingartner et al., 1998; 2005; 2013). Based on previous studies, the region south of Hanna Shoal is thought to be much more oceanographically stable than the surrounding waters (Weingartner et al., 1998; 2005; 2013). The later years of this present study had colder bottom water overall than in the earlier years, suggesting cold winter water was not fully flushed out of the system in the summer. Cold bottom waters have been recorded previously in summer months on Hanna Shoal; however, these conditions are not constant, varying nearly 4°C from year to year (Weingartner et al., 2013). Temperature changes have implications for the benthic community, since many biological processes are temperature dependent. Recent evidence has suggested that there has been a 50% increase of flow through the Bering Strait over the past decade (Woodgate et al., 2012). Increased flow has led to an increase in heat and freshwater fluxes into the Chukchi Sea (Woodgate et al., 2012), and a coarser sediment grain size (Grebmeier and Cooper, 1995).

Changes in the drivers that structure the epibenthic communities were seen in this study, and their importance in describing epibenthic variability remained high for all years.

One environmental driver that was not examined in the current study, but that may impact the Chukchi Sea, is sea ice (Gutt, 2001). Sea ice in the northern hemisphere ranges from year-round thick ice (rarely exceeds depths > 40 m) to thin seasonal ice (on average 0.5-2 m) that only occurs in the winter months (Gutt, 2001). Thick ice prevents sunlight from reaching the sea surface, which in turn prevents photosynthesis and development of an underlying ice algal layer (Fisher et al., 1988; Fortier et al., 2002). When thick ice is present, there is little flux of particulates to the benthos. When the ice thins, ice algae are exposed to adequate sunlight for photosynthesis, seeding the phytoplankton bloom in the spring. The seasonal flux in ice melt timing as well as direction will cause considerable variation in magnitude and location of epibenthic communities (Fisher et al., 1988; Fortier et al., 2002). Ice scour is another physical driver of epibenthic communities in the Chukchi Sea since it is a shallow shelf system. Ice drift is mainly current driven and can run aground at depths of 600 m, leaving deep gouges (Sanderson, 1988; Gutt, 2001). In the Canadian Arctic, a benthic community that was once dominated by suspension feeders shifted to a community of scavengers and deposit feeders after scour occurred (Conlan et al., 1998; Gutt, 2001; Conlan and Kvitek, 2005). Scour has the potential to increase diversity within the system when different recolonization stages coexist, and scour can open up space for organisms (Gutt, 2001). Ice presence could therefore explain some variability seen in the biological community from 2009 to 2013.

5. Conclusion

The present study observed significant differences of the epibenthic community in the Chukchi Sea from 2009 to 2013. Ophiuroidea and Crustacea were the two taxa that contributed most to abundance and biomass; however, contributions of *Chionoecetes opilio,* Caridea, and *Pagurus* spp. to the communities were more variable over time. The environmental drivers that best described community structure were bottom water temperature, salinity, dissolved oxygen, mean sediment chlorophyll *a*, and sediment grain size and organic matter. Of these, sediment grain size was a consistent driver in all years of the study, and likely had a minimal impact on the differences in epibenthic communities among years. The variability observed in the epibenthic community could be due to a shift in current regime and water mass characteristics, which could

have led to a slower flushing of winter water from the area. It is this cold water that determines the recruitment success of various organisms, including Caridea and crab larvae. However, the Chukchi Sea ecosystem is highly dynamic, and, therefore, the variability seen in this study could be due to natural system variability as well, but more testing is needed to confirm this.

6. References

Anderson, P.J., 2000. Pandalid shrimp as indicators of ecosystem regime shift. J Northw Atl Fish Sci. 27, 1-10.

Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar Ecol Prog Ser. 189, 117-123.

Arrigo, K.R., van Dijken, G.L., 2004. Annual cycles of sea ice and phytoplankton in Cape Bathurst polynya, southeastern Beaufort Sea, Canadian Arctic. Geophys Res Lett. DOI: 10.1029/2003GL018978.

Balazy, P., Kuklinski, P., Włodarska-Kowalczuk, M., Barnes, D., Kędra, M., Legeżyńska, J., Węsławski, J.M., 2015. Hermit crabs (*Pagurus* spp.) at their northernmost range: distribution, abundance and shell use in the European Arctic. Polar Res. Doi: http://dx.doi.org/10.3402/polar.v34.21412.

Baldwin, R.J., Smith Jr., K.L., 2003. Temporal dynamics of particulate matter fluxes and sediment community response in Port Foster, Deception Island, Antarctica. Deep Sea Res Pt II. 50, 1707-1725.

Blanchard, A.L., Feder, H.M., 2014. Interactions of habitat complexity and environmental characteristics with macrobenthic community structure at multiple spatial scales in the northeastern Chukchi Sea. Deep Sea Res Pt II. Doi: 10.1016/j.dsr2.2013.09.022.

Blanchard, A.L., Parris, C.L., Knowlton, A.L., Wade, N.R., 2013a. Benthic ecology of the northeastern Chukchi Sea. Part II. Spatial variation of megafaunal community structure, 2009-2010. Cont Shelf Res. 67, 67-76.

Blanchard, A.L., Parris, C.L., Knowlton, A.L., Wade, N.R., 2013b. Benthic ecology of the northeastern Chukchi Sea. Part I. Environmental characteristics and macrofaunal community structure, 2008-2010. Cont Shelf Res. 67, 52-66.

Bluhm, B.A., Iken, K., Hardy, S.M., Holladay, B.A., 2009. Community structure of epibenthic megafauna in the Chukchi Sea. Aquat Biol. 7, 269-293.

Bluhm, B.A., Piepenburg, D., von Juterzenka, K., 1998. Distribution, standing stock, growth, mortality, and production of *Strongylocentrotus pallidus* (Echinodermata: Echinoidea) in the northern Barents Sea. Polar Biol. 20, 325-334.

Boos, K., Franke, H.D., 2004. Abundance and distribution of ophiuroids off Helgoland, German Bight (North Sea), in: Heinzeller, T., Nebelsick, J.H., (Eds.) Echinoderms: Munchen. Taylor & Francis Group plc, London, UK, pp 157-158.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User manual/tutorial, in: PRIMER-E, Plymouth.

Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: The regional physical oceanography. Seattle, Washington, USA. Pp 111-131.

Coachman, L.K., Barnes, C.A., 1963. The movement of Atlantic water in the Arctic Ocean. ANIA. Doi: http://dx.doi.org/10.14430/arctic3517.

Conlan, K.E., Lenihan, H.S., Kvitek, R.G., Oliver, J.S., 1998. Ice scour disturbance to benthic communities in the Canadian high Arctic. Mar Ecol Prog Ser. 166, 1-16.

Conlan, K.E., Kvitek, R.G., 2005. Recolonization of soft-sediment ice scours on an exposed Arctic coast. Mar Ecol Prog Ser. 286, 21-42.

Cooper, L.W., Grebmeier, J.M., Larson, I.L., Egorov, V.G., Theodorakis, C., Kelly, H.P., Lovvorn, J.R., 2002. Seasonal variation in sedimentation of organic materials in the St. Lawrence Island polynya region, Bering Sea. Mar Ecol Prog Ser. 226, 13-26.

Day, R.H., Weingartner, T.J., Hopcroft, R.R., Aerts, A.M., Blanchard, A.L., Gall, A.E., Gallaway, B.J., Hannay, D.E., Holladay, B.A., Mathis, J.T., Norcross, B.L., Questel, J.M., Wisdom, S.S., 2013. The offshore northeastern Chukchi Sea, Alaska: A complex high-latitude ecosystem. Cont Shelf Res. 67, 147-165.

Dionne, M., Sainte-Marie, B., Bourget, E., Gilbert, D., 2003. Distribution and habitat selection of early benthic stages of snow crab *Chionoecetes opilio*. Mar Ecol Prog Ser. 259, 117-128.

Dunton, K.H., Goodall, J.L., Schonberg, S.V., Grebmeier, J.M., Maidment, D.R., 2005. Multi-decadal synthesis on benthic-pelagic coupling in the western Arctic: Role of cross-shelf advective processes. Deep Sea Res Pt II. 52, 3462-3477.

Ernst, B., Orensanz, J.M., Armstrong, D.A., 2005. Spatial dynamics of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. Can J Fish Aquat Sci. 62, 250-268.

Ernst, B., Armstrong, D.A., Burgos, J., Orensanz, J.M., 2012. Life history schedule and periodic recruitment of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. Can J Fish Aquat Sci. 69, 532-550.

Etter, R.J., Grassle, J.F., 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. Nature. 360, 576-578.

Fay, F.H., 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. N Am Fauna. 74, 1-279.

Feder, H.M., Naidu, A.S., Jewett, S.C., Hameedi, J.M., Johnson, W.R., Witledge, T.E., 1994. The northeastern Chukchi Sea: Benthos-environmental interactions. Mar Ecol Prog Ser. 111, 171-190.

Feder, H.M., Jewett, S.C., Blanchard, A., 2005. Southeastern Chukchi Sea (Alaska) epibenthos. Polar Biol. 28, 402-421.

Fisher, G., Fütterer, D., Gersonde, R., Honjo, S., Ostermann, D., Wefer, G., 1988. Seasonal variability of particle flux in the Weddell Sea and its relation to ice cover. Nature. 335, 426-428.

Fortier, M., Fortier, L., Michel, C., Legendre, L., 2002. Climatic and biological forcing of the vertical flux of biogenic particles under seasonal Arctic sea ice. Mar Ecol Prog Ser. 225, 1-16.

Grebmeier, J.M., 1987. The ecology of benthic carbon cycling in the northern Bering and Chukchi Seas. PhD Thesis University of Alaska, Fairbanks.

Grebmeier, J.M., Barry, J.P., 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: A benthic perspective. J Marine Syst. 2, 495-518.

Grebmeier, J.M., Cooper, L.W., 1995. Influence of the St. Lawrence Island Polynya upon the Bering Sea benthos. J Geophys Res-Oceans. 100, 4439-4460.

Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006. Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi Seas in the Amerasian Arctic. Prog Oceanogr. 71, 331-361.

Grebmeier, J.M., Feder, H.M., McRoy, C.P., 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. II. Benthic community structure. Mar Ecol Prog Ser. 51, 253-268.

Grebmeier, J.M., McRoy, C.P., Feder, H.M,. 1988. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi seas. 1. Food supply source and benthic biomass. Mar Ecol Prog Ser. 48, 57-67.

Gunderson, D.R., Ellis, I.E., 1986. Development of a plumb staff beam trawl for sampling demersal fauna. Fish Res. 4, 35-41.

Gutt, J., 2001. On the direct impact of ice on marine benthic communities, a review. Polar Biol. 24, 553-564.

Haflinger, K., 1981. A survey of benthic infaunal communities of the southeastern Bering Sea, in: Hood, D.W., Calder, J.A., (Eds.) The eastern Bering Sea shelf: Oceanography and resources, Vol 2. Univ Wash Press, Seattle, Washington, pp 1091-1104.

Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog Oceanogr. 47, 103-145.

Highsmith, R.C., Coyle, K.O., 1992. Productivity of Arctic amphipods relative to gray whale energy requirements. Mar Ecol Prog Ser. 83, 141-150.

Incze, L.S., Armstrong, D.A., Smith, S.L., 1987. Abundance of larval Tanner crabs (*Chionoecetes* spp.) in relation to adult females and regional oceanography of the southeastern Bering Sea. Can J Fish Aquat Sci. 44, 1143-1156.

Jay, C.V., Fischbach, A.S., Kochnev, A.A., 2012. Walrus areas of use in the Chukchi Sea during sparse sea ice cover. Mar Ecol Prog Ser. Doi: 10.3354/meps10057.

Johannessen, O.M., Bengtsson, L., Miles, M.W., Kuzmina, A.I., Semenov, V.A., Alekseev, G.V., Nagurnya, A.P., Zakharov, V.F., Bobylev, L.P., Pettersson, L.H., Hasselmann, K., Cattle, H.P., 2004. Arctic climate change: Observed and modelled temperature and sea-ice variability. Tellus A. 56, 328-341.

Konar, B., Ravelo, A., Grebmeier, J., Trefry, J.H., 2014. Size frequency distributions of key epibenthic organisms in the eastern Chukchi Sea and their correlations with environmental parameters. Deep Sea Res Pt II. 102, 107-118.

Martin, S., Drucker, R., 2012. The effects of possible Taylor columns on the summer ice retreat in the Chukchi Sea. J Geophys Res. 102, 10473-10482.

McMahon, K.W., Ambrose, W.G., Johnson, B.J., Sun, M., Lopez, G.R., Clough, L.M., Carroll, M.L., 2006. Benthic community response to ice algae and phytoplankton in Ny Alesund, Svalbard. Mar Ecol Prog Ser. 310, 1-14.

Moore, S.E., Huntington, H.P., 2008. Arctic marine mammals and climate change: Impacts and resilience. Ecol Appl. 18, 157-165.

Overland, J., Rodionov, S., Minobe, S., Bond, N., 2008. North Pacific regime shifts: Definitions, issues and recent transitions. Prog Oceanogr. 77, 92-102.

Parada, C., Armstrong, D.A., Ernst, B., Hinckley, S., Orensanz, J.M., 2010. Spatial dynamics of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea – Putting together the pieces of the puzzle. Bull Mar Sci. 86, 413-437.

Piepenburg, D., 2000. Arctic brittle stars (Echinodermata: Ophiuroidea), in: Gibson, R.N., Barnes, M., (Eds.), Oceanography and marine biology: An annual review volume 38. Taylor & Francis Inc., New York, NY, pp 189-256.

Piepenburg, D., Blackburn, T.H., von Dorrien, C.F., Gutt, J., Hall, P.O.J., Hulth, S., Kendall, M.A., Opalinski, K.W., Rachor, E., Schmid, M.K., 1995. Partitioning of benthic community respiration in the Arctic (northwestern Barents Sea). Mar Ecol Prog Ser. 118, 199-213.

Piepenburg, D., 2006. The seafloor fauna in a changing Arctic – a review on its past, present, and future. Polarforschung. 75, 63-76.

Piepenburg, D., Schmid, M.K., 1996. Brittle star fauna (Echinodermata: Ophiuroidea) of the Arctic northwestern Barents Sea: Composition, abundance, biomass, and spatial distribution. Polar Biol. 16: 383-392.

Questel, J.M., Clarke, C., Hopcroft, R.R., 2013. Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. Cont Shelf Res. 67, 23-41.

Ravelo, A.M., Konar, B., Trefry, J.H., Grebmeier, J.M., 2014. Epibenthic community variability in the northeastern Chukchi Sea. Deep Sea Res Pt II. Doi: 10.1016/j.dsr2.2013.07.017.

Ruhl, H.A., 2007. Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific. Ecology. 88, 1250-1262.

Sanderson, T.J., 1988. Ice mechanics and risks to offshore structures. Graham and Trotman, London.

Semtner Jr., A.J., 1987. A numerical study of sea ice and ocean circulation in the Arctic. J Phys Oceanogr. 17, 1077-1099.

Somerton, D.A., 1981a. Life history and population dynamics of two species of Tanner crab, *Chionoecetes bairdi* and *C.opilio*, in the eastern Bering Sea with implications for the management of the commercial harvest. PhD thesis, University of Washington, Seattle, Washington.

Somerton, D.A., 1981b. Regional variation in the size at maturity of two species of Tanner Crab (*Chionoecetes bairdi* and *C.opilio*) in the eastern Bering Sea, and its use in defining management subareas. Can J Fish Aquat Sci. 38, 163-174.

Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern Bering Sea-III. Patterns of primary production. Cont Shelf Res. 13, 575-599.

Stoker, S.W., 1981. Benthic invertebrate macrofauna of the eastern Bering/Chukchi continental shelf: oceanography and resources, Vol. 2. Univ Wash Press, Seattle, Washington, pp 1069-1090.

Stroeve, J., Holland, M.M., Meier, W., Scambos, T., Serreze, M., 2007. Arctic sea ice declines: Faster than forecast. Geophys Res Lett. Doi: 10.1029/2007GL029703.

Summers, A.C., Nybakken, J., 2000. Brittle star distribution patterns and population densities on the continental slope off central California (Echinodermata: Ophiuroidea). Deep Sea Res Pt II. 47, 1107-1137.

Taghon, G.L., 1982. Optimal foraging by deposit-feeding invertebrates: Roles of particle size and organic coating. Oecologia. 52, 295-304.

Tenore, K.R., 1988. Nitrogen in benthic food chains, in: Blackburn, T.H., Sørensen, J., (Eds.), Nitrogen cycling in coastal marine environment. John Wiley & Sons Ltd, pp 191-206.

Walsh, J.E., 1978. Temporal and spatial scales of the Arctic circulation. Mon Weather Rev. 106, 1532-1544.

Wassmann, P., 1991. Dynamics of primary production and sedimentation in shallow fjords and polls of western Norway. Oceanogr Mar Biol. 29, 87-154.

Wassmann, P., Slagstad, D., Riser, C.W., Reigstad, M., 2006. Modelling the ecosystem dynamics of the Barents Sea including the marginal ice zone: II. Carbon flux and interannual variability. J Mar Sys. 59, 1-24.

Weingartner, T., Aagaard, K., Woodgate, R., Danielson, S., Sasaki, Y., Cavalieri, D., 2005. Circulation on the north central Chukchi Sea shelf. Deep Sea Res Pt II. 52, 3150-3174.

Weingartner, T.J., Cavalieri, D.J., Aagaard, K., Sasaki, Y., 1998. Circulation, dense water formation, and outflow on the northeast Chukchi shelf. J Geophys Res – Oceans. 103, 7647-7661.

Weingartner, T., Dobbins, E., Danielson, S., Winsor, P., Potter, R., Statscewich, H., 2013. Hydrographic variability over the northeastern Chukchi Sea shelf in summer-fall 2008-2010. Cont Shelf Res. 67, 5-22.

White, M.G., 1977. Ecological adaptations by Antarctic poikilotherms to the polar marine environment, in: Liano, G.A., (Eds.) Adaptations within Antarctic ecosystems. Gulf Publishing Co, Houston, pp 197-208.

White, D., Kimerling, J.A., Overton, S.W., 1992. Cartographic and geometric components of a global sampling design for environmental monitoring. Cart Geogr Inform. 19, 5-22.

Williams, J.D., McDermott, J.J., 2004. Hermit crab biocoenoses: A worldwide review of the diversity and natural history of hermit crab associates. J Exp Mar Biol Ecol. 305, 1-128.

Winsor, P., Chapman, D.C., 2002. Distribution and interannual variability of dense water production from coastal polynyas on the Chukchi Shelf. J Geophys Res-Oceans. Doi: 10.1029/2001JC000984.

Woodgate, R.A., Weingartner, T.J., Lindsay, R., 2012. Observed increases in Bering Strait oceanic fluxes from the Pacific to the Arctic from 2001 to 2011 and their impacts on the Arctic Ocean water column. Geophys Res Lett. Doi: 10.1029/2012GL054092.